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ON THE AREAS OF THE AXIS CYLINDER AND MEDULLARY SHEATH AS SEEN IN CROSS SECTIONS OF THE SPINAL NERVES OF VERTEBRATES.

By Henry H. Donaldson and G. W. Hoke.

(*From the Neurological Laboratory of the University of Chicago.*)

With one figure.

Introduction.—The results presented in this paper are, in each case, based on averages of the measurements of twenty or more spinal nerve fibers. The nerves were taken from various animals representing the five great classes of vertebrates. The measurements show that the areas of the medullary sheath and enclosed axis are nearly equal, and by consequence that the volume of the substance forming the axis cylinders is equal to that forming the medullary sheaths. The relation constitutes a point of similarity remarkable for its wide extension through the vertebrate series.[1] It enables us, moreover, to estimate in any nerve the volume of the substance specialized for the conduction of the nerve impulse. Since this quantitative relation between axis cylinder and sheath is so close, it strongly suggests that in some way the axis controls the formation of the surrounding medullary substance.

In the spinal nerves of some animals this relation, as expressed by the equal areas of the axis and sheath when the fibers are seen in the cross section, was pointed out several years ago

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[1] The Acrania and Cyclostomi do not develop medullary sheaths on their nerve fibers, and are therefore not included.

(DONALDSON, 1895, p. 154).   The fact that it was maintained
in the growing fiber was also noted (DONALDSON, 1901, p. 180;
1901, A, p. 326); and later DUNN ('00, '02) verified the relation
by the study of the medullated fibers in the sciatic nerve of the
frog.   It seemed desirable, however, to extend the observations
on this point, and in 1901, Mr. HOKE took up the question and
determined the relative area of the axis and sheath in cross sec-
tions of fibers from the nerves of 27 species of vertebrates rep-
resenting the five great classes.[1]

Technique.—The animals were killed with chloroform.
The nerve, usually from the brachial plexus, laid bare and par-
tially fixed *in situ* with osmic acid (1 % sol.).   After half an
hour the nerve was removed on a piece of cardboard to prevent
shrinking, and replaced in a 1 % solution of osmic acid for 24
hours.   Then imbedded in paraffin by the usual method.   The
sections were cut 3.5 μ thick and mounted in colophonium.

The measurements of the large fibers were made under the
magnification of 340 diameters, or, in some cases, 265 diame-
ters.   The very small fibers were measured with the 1-12 oil
immersion.

*The Effect of Osmic Acid Treatment upon the Size of
Medullated Peripheral Nerves.*—This reaction was studied be-
cause of its obvious bearing upon the observations here pre-
sented.

BOLL ('76) states that 1 % osmic acid causes a swelling of
the sheath to almost double its normal size.   This, however,
was the result of putting a fiber which had been *teased out
while fresh*, in a drop of the acid and examining it after a short
time.   Prolonged immersion in osmic, he says, in the same
place, is followed by a shrinkage of the fiber.   These statements
lose value by reason of the fact that teasing out the fresh fibers
stretches them and thus alters their reaction to the reagent.

BOVERI ('85) concludes that the normal form and structure
of the medullary sheath is very little modified by the osmic acid

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[1] Mr. HOKE'S account of his work was accepted as a thesis for the degree of
Master of Science in the department of Neurology of the University of Chicago
in 1902.   The data in that thesis form the basis of the present paper.

treatment, and this view is shared by a number of other ob-
servers who have studied this question. The method employed
in this investigation was practically the same as that used by
BOVERI.

Speaking generally, it may be said that mistreatment tends
to cause a swelling of the medullated fiber (in 1 % osmic acid)
in which the sheath becomes somewhat more swollen than the
axis. The most reliable measurements, therefore, are those
made on nerves which have suffered the least mechanical dam-
age.

To determine whether our method of treatment produced
permanent alteration in the size of the nerves used, a series of
observations was made upon the eighth, ninth and tenth spinal
nerves running free along the dorsal wall of the body cavity of
the frog, and also on the sciatic nerves of the white rat.

The nerves were laid bare and a bristle bent in the
form of the letter U, exerting a tension of .25 to .40 grams,
according to the size of the nerve, was rapidly tied to either
end of the nerve. In this way about one centimeter of nerve was
included between the ends of the bristle. The nerve thus prepared
was then removed and before putting it in any fluid its diameter
was carefully measured under the microscope. It was then
placed for twenty-four hours in a shallow cell containing osmic
acid. The subsequent treatment was exactly similar to that
given under the paragraph on technique. Bristle and attached
nerve were finally mounted in colophonium and the diameter
again carefully measured.

The results of these observations are presented in Table I
for the Frog and Table II for the Rat.

The column on the left gives the diameter in μ of the fresh
nerves with the bristle attached. On the right is given the di-
ameters in μ while the nerves are in colophonium, after com-
plete treatment by the osmic acid method as described above.
In Table I, the middle column introduces the diameter of the
nerves after having been in osmic acid twenty-four hours. The
final number at the foot of each column gives the square of the
average radius. This number, when multiplied by π would

give in sq. μ the total area of the nerves measured.   As indicated, the nerves of the frog have increased in area 2.4%, those of the rat, .57%.

The measurements upon the rat were the last made, after some skill had been acquired in this manipulation, and are probably the more reliable.

TABLE I.

To show the effect of the technique upon the eighth, ninth and tenth spinal nerves of the Frog.   Seven specimens.

Diameter in μ. Fresh Fiber, Bristle Attached.	Diameter in u. After Being in Osmic Acid ₁% 24 hrs.	Diameter in μ. In Colophonium.
456.00	498.75	456.00
513.00	541.50	527.25
541.50	570.00	541.25
627.00	701.25	641.25
470.25	470.00	484.50
427.50	441.75	427.50
498.75	527.25	498.75

Av. Diam.   504.85   538.80   510.95
Av. Radii Squared   63716.85 sq. μ 65264.92 sq. μ
Percentage difference + 2.4%.

TABLE II.

To show the effect of the technique upon the sciatic nerve of the White Rat.   Nine specimens.

Diameter in μ. Fresh Fiber, Bristle Attached.	Diameter in μ. In Colophonium.
1026.0	1062.0
926.0	969.0
1282.5	1282.5
912.0	926.0
912.0	883.5
1154.0	1168.0
997.5	969.0
1140.0	1140.0
997.5	983.0

Av. Diam.   1039.5   1042.5
Av. Radii Squared 1080560.2 sq. μ 1086806.2 sq. μ
Percentage difference + .57%.

The results of these observations seem to justify the conclusion that the osmic acid treatment, followed by the preparation for examination, produces but little change from the normal diameter (or area) of peripheral nerve fibers.

Conditions Determining the Choice of the Fibers to be Measured.—There were used for measurement only those fibers which had been cut at right angles to their long axis and which stood vertically. It is easy to see that any departure of a fiber from the vertical would make the measurements for the thickness of the sheath too large, and those for the axis correspondingly too small. From measurement were excluded those fibers in which the medullary sheath appeared double, as occasionally occurs when the fiber has been cut through an enlarged cleft of LANTERMANN.

The rare instances in which the section passes through an internodal nucleus, or just above or below a node—where the relative area of the medullary sheath is very greatly increased— were easily avoided. A fiber in which the sheath was wrinkled, or which departed much from the circular form, was not measured. Where the section of the nerve fiber was suitable in other respects—and at the same time was slightly oval—two diameters were taken and the mean taken as the value to be used. Among the small fibers those that were stained gray and not black were classed as immature, and were not measured. It is among the small fibers that the greatest normal range in the relative development of the medullary sheath appears, and it is here too, that the greatest difficulties in making exact measurements are met, any departure from the vertical being especially disturbing.

The very small medullated fibers which appear in the rami communicantes were not studied in this investigation.

Method of Measurement.—On sections of fibers thus prepared and thus selected, the diameter of the entire fiber was first measured and then the diameter of the axis. In order to give an idea of this procedure we may take as an example the first group of ten measurements, the final results of which appear in Table VI after Specimen I. In the first column of Table

III (see below) is given under A + S, (axis + sheath), the total diameter of each fiber, while under A (axis) is given the diameter of the axis. The two columns to the right give the corresponding radii. The measurements were first put down in terms of the divisions of the ocular micrometer—the subdivisions being estimated to tenths of these units.

TABLE III.

Diameters and Radii of entire fibers and axes, in divisions of the ocular micrometer.

Diameter		Radii	
A + S	A	A + S	A
4.0	2.9	2.00	1.45
4.0	2.9	2.00	1.45
4.7	3.1	2.35	1.55
4.2	3.1	2.10	1.55
5.0	3.6	2.50	1.80
5.0	3.8	2.50	1.90
5.0	3.3	2.50	1.65
4.5	3.2	2.25	1.60
4.9	3.2	2.45	1.60
4.8	3.2	2.40	1.60

To transform these measurements into μ we multiply in each instance by the value of one division of the ocular micrometer which in this case was 3.06 μ. As the radii alone will be used, they only are reduced to μ. (See Table IV.)

TABLE IV.

A + S	A
6.12	4.43
6.12	4.43
7.19	4.74
6.45	4.74
7.65	5.50
7.65	5.81
7.65	5.04
6.88	4.89
7.49	4.89
7.24	4.89

It is on the basis of these radii that we calculate the areas of the fibers and of their axes, and for this we employ the formula πr^2 giving π the value of 3.14.

As the square of the average radius for the group is not equivalent to the average of the squares of the radii, and as the

latter is the number desired, it is necessary first to find the square of the radius in the case of each of these ten fibers ; then to take the average of these squares and multiply by π in order to obtain the average area of the fibers.

TABLE V.

The squares of the foregoing radii are as follows :

(Radius A + S)²	(Radius A)²
37.21	19.62
37.21	19.62
51.84	22.46
40.96	22.46
57.76	30.25
57.76	33.75
57.76	25.40
46.24	23.91
54.76	23.91
51.84	23.91

	(Radius A + S)²	(Radius A)²
Total	493.34 sq. μ	245.29 sq. μ
Average	49.33 sq. μ	24.53 sq. μ

The average for the squares of the radii in the case of the axis and sheath and of the axis alone, must be multiplied by π (= 3.14) to give in square μ the areas of the entire fiber and of the axis respectively. In this instance the areas are as follows:

Areas.

Entire Fiber	Axis
154.9 sq. μ	76.99 sq. μ

The object of this investigation is to determine whether in the cross section of the fiber the area occupied by the ring-like sheath is equal to that of the enclosed axis.

By hypothesis they should be equal in area, hence in the case of the average entire fiber containing 154.9 sq. μ in its section we should expect to find one-half of this area $\frac{154.9}{2} = 77.5$ sq. μ in the axis and the other half in the sheath.

With this ideal area, the area of the axis as observed is compared. Thus: Estimated area of sheath = 77.5 sq. μ.
Observed " axis = 76.99 sq. μ.

According to the hypothesis, the area of the axis should equal that of the sheath. The observed area of the axis is seen to be less by 0.51 sq. μ, or using the ideal area of the sheath

as the standard, it is less by 0.6%. In this particular group, therefore, the actual area of the sheath is 0.6% greater than it would be if the assumed one to one relation of the axis and sheath were maintained.

In working out the results, it is this ideal of one-half the area of the total fiber which is always taken as the standard, and the observed area of the axis is compared with it. If the area of the axis is less than one-half the area of the total fiber, then it follows that the sheath must have been *more* than one-half and the percentage value of the difference is written in plus, to show that the sheath is too large by this amount, or, under the reverse conditions, as minus, to show that it is too small. This difference is designated the average percentage deviation.

In the case of each of the 1540 fibers here presented (Table VI) calculations similar to those just given, have been made. It is thus possible to say in each instance by what percentage the area of the sheath departs from that of the ideal, although in the table only the percentages for the extreme cases and for the average deviation are given.

Description of the Material Employed.—The following list of the specimens gives the common name ; scientific name (entered only once where several specimens of the same species were examined); length of body; weight; sex; age; season when killed; nerves taken; locality; and by whom prepared. Where no statement is made; the sex is male; the season winter; the nerves are taken from the brachial plexus, and the material killed and prepared by Mr. HOKE in this laboratory. The omission of any of the other data means that they are not available.

TABLE VI.

	Animal	Specimen	Number of fibers measured	Average diameter of fibers in μ	Extreme percentage — or + deviation in each series —	+	Average percentage deviation per fiber —	or +
Fish	Shark	I	40	13.6	15.0	15.5		0.62
		II	50	15.0	{ 22.2	15.5	3.00	
					{ 22.0	2.6		0.50
	Skate	III	40	19.6	21.6	15.0	1.30	
		IV	40	20.5	18.9	21.8		0.40
		V	30	21.8	22.2	35.5	2.90	
	Flounder	VI	40	17.0	23.4	13.0		
		VII	40	16.1	21.2	25.0		0.50
		VIII	40	15.9	12.5	19.9		2.40
Amphibia	Frog	IX	20	14.2	21.9	26.8	2.00	
		X	30	14.7	21.6	24.0	0.80	
		XI	20	13.9	7.5	3.7	1.20	
		XII	20	13.3	13.4	9.2	2.30	
		XIII	20	15.9	5.0	11.6		1.90
		XIV	20	12.5	12.5	8.1	0.20	
		XV	20	11.9	22.4	17.9	2.60	
		XVI	20	13.5	19.2	8.0	1.79	
	Toad	XVII	40	11.2	14.5	14.0	0.30	
	Mud Puppy	XVIII	40	10.3	20.0	18.2	0.30	
Reptiles	Lizard	XIX	40	9.8	10.0	20.0		3.00
	Horned Toad	XX	40	6.2	11.1	12.2	0.52	
	Anolis	XXI	40	7.7	10.0	20.0		0.90
	Turtle	XXII	40	12.4	21.8	24.2		1.00
Birds	Duck	XXIII	40	5.8	16.7	20.1	2.00	
	Chick	XXIV	40	11.6	12.5	12.5	1.60	
	Dove	XXV	40	12.8	30.0	18.0	1.50	
Mammals	White Rat	XXVI	40	10.1	19.5	22.1		4.20
		XXVII	20	5.6	16.7	22.0	0.60	
		XXVIII	30	4.0	28.3	18.6		0.90
		XXIX	20	5.0	17.8	19.8		3.50
		XXX	20	11.1	5.0	11.1		2.70
		XXXI	20	12.8	7.2	6.6	1.60	
		XXXII	40	13.0	12.8	17.7	1.10	
	Rabbit	XXXIII	40	13.3	27.5	24.5	0.80	
	Agouti	XXXIV	40	13.1	23.7	11.1		2.90
	Bear	XXXV	40	11.7	14.4	12.5		2.09
	Fox	XXXVI	40	13.3	7.2	23.2		5.40
	Dog	XXXVII	40	11.6	16.0	16.5		0.90
	Wild Cat	XXXVIII	40	13.7	10.3	11.1		3.80
	Cat	XXXIX	40	16.0	14.2	15.0	1.30	
	Manila Monkey	XL	40	10.7	11.1	13.5		0.50
	Spider Monkey	XLI	40	11.3	13.7	18.6		0.80
	Rhesus	XLII	40	10.9	7.7	14.1		1.00
	Ape	XLIII	40	12.3	16.7	23.7		3.90
	Baboon	XLIV	40	11.0	7.2	11.6		1.30
	Man	XLV	40	13.9	11.1	19.2		0.70

1540

For the 1540 fibers the average percentage deviation $= + 0.45\%$.

Description of Specimens on which Measurements have been made.

Specimen 1. Dog Shark (*Mustelus canis*), length 95 cm., summer, Woods Holl.

Specimen 2. Dog Shark, length 95 cm., summer, Woods Holl.

Specimen 3. Common Skate (*Raja erinacea*), length 49 cm., female, summer, Woods Holl.

Specimen 4. Common Skate, length 48 cm., female, summer, Woods Holl.

Specimen 5. Common Skate, length 45 cm., female, summer, Woods Holl.

Specimen 6. Summer Flounder (*Paralicthys dentatus*), length 40 cm., female, summer, Woods Holl.

Specimen 7. Summer Flounder, length 49 cm., summer, Woods Holl.

Specimen 8. Summer Flounder, length 49 cm., summer, Woods Holl.

Specimen 9. Frog (*Rana virescens*), body-weight 22 grms., sciatic nerve, summer.

Specimen 10. Frog, body-weight 49.8 grms., sciatic nerve.

Specimen 11. Frog, body-weight 31 grms., second spinal nerve.

Specimen 12. Frog, body-weight 31 grms., 8th spinal nerve.

Specimen 13. Frog, body-weight 74.5 grms., female, second spinal nerve.

Specimen 14. Frog, body-weight 74.5 grms., female, 8th spinal nerve.

Specimen 15. Frog, body-weight 74.5 grms., female, dorsal root of the 7th spinal nerve.

Specimen 16. Frog, body-weight 74.5 grms., female, ventral root of the 7th spinal nerve.

Specimen 17. Toad (*Bufo lentiginosus*), sciatic nerve, summer.

Specimen 18. Mud-Puppy (*Necturus maculatus*) female, length 18 cm., summer.

Specimen 19. Common Lizard (*Sceloporus undulatus*), weight 8.2 grms.

Specimen 20. Horned Toad (*Phrynosoma cornutum*), hybernating.

Specimen 21. American Chameleon (*Anolis principalis*), weight 2.55 grms.

Specimen 22. Turtle (*Chrysemys marginata*).

Specimen 23. Domestic Duck, female, 3 weeks old.

Specimen 24. Chick, female, young.

Specimen 25. Pigeon (*Columba livia*).

Specimen 26. White Rat (*Mus rattus var. albus*), body-weight 104 grms.

Specimen 27. White Rat, body-weight 10 grms., 6th cervical nerve.

Specimen 28. White Rat, body-weight 10 grms., 4th thoracic spinal nerve.

Specimen 29. White Rat, body-weight 10 grms., 2nd lumbar nerve.

Specimen 30. White Rat, body-weight 25 grms., 6th cervical nerve.

Specimen 31. White Rat, body-weight 65 grms., 6th cervical nerve.

Specimen 32. White Rat, body-weight 150 grms., 6th cervical nerve.

Specimen 33. Rabbit (*Lepus cuniculus*), adult, male.

Specimen 34. Agouti (*Dascyprocta aguti*), weight 1350 grms., Dr. HARDESTY, San Francisco.

Specimen 35. Black Bear (*Ursus americanus*), Dr. HARDESTY, San Francisco.

Specimen 36. Gray Fox (*Urocyon cinero-argentatus*), body-weight 3940 grms.,
Dr. Hardesty, San Francisco.

Specimen 37. Shepherd Dog, male.

Specimen 38. Wild Cat (*Felis rufus*), body-weight 3050 grms., Dr. Hardesty, San Francisco.

Specimen 39. Cat (*Felis domesticus*), male.

Specimen 40. Manila Monkey (*Macacus cynomolgus*), body-weight 965 grms., Dr. Hardesty, San Francisco.

Specimen 41. Spider Monkey (*Ateles paniscus*), body-weight 1650 grms., Dr. Hardesty, San Francisco.

Specimen 42. Rhesus Monkey (*Macacus rhesus*), body-weight 2720 grms. Dr. Hardesty, San Francisco.

Specimen 43. Black Coated Ape (*Macacus inuus*), body-weight 5216 grms., Dr. Hardesty, San Francisco.

Specimen 44. Baboon (*Cynocephalus babuin*), body-weight 6247 grms., Dr. Hardesty, San Francisco.

Speciman 45. Man, adult, sciatic nerve.

Accuracy of Measurements and Sources of Error.—In estimating the value of the measurements given in Table VI, it is to be remembered that with the magnification most commonly used for the larger fibers, one-tenth of a division of the ocular micrometer or 0.306 μ was a shade over 3% of the diameter of a fiber 10 μ in thickness. In case, therefore, that a fiber was measured as 9.7 μ or 10.3 μ instead of 10 μ, the deviation in the resulting areas from that based on 10 μ would be approximately, ± 6%. Individual cases might, therefore, readily vary by this amount as an error of observation.

With fibers of greater diameter the relative value of this error would decrease, while with those of less diameter it would increase. Similarly with the higher magnification used for the smaller fibers, the value of the one division of the ocular micrometer was 1.42 μ, and one-tenth, or 0.142 μ would be 3% of a fiber 4.7 μ in diameter. In this case also the error of one-tenth of a division in the reading, either plus or minus, would give rise to corresponding deviations in the resultant areas, with a relative decrease as the fibers become larger and an increase as they become smaller.

In general, therefore, the errors of observation would increase as the fibers diminished in diameter. Such errors, however, would tend in all cases to balance out and so be reduced as the number of observations becomes large.

Thus when we take the difference between the sum of all the minus percentages and the sum of all the plus percentages by which the sheath differs from the ideal half of the area of the entire fiber, we find that for the 1540 fibers, this amounts on the average to + .45 %. That is, on the average in this series, the area of the medullary sheath exceeds the ideal half by + .45%, or one-thirteenth of ± 6%, the deviation which might be expected as an error of observation in the case of a single fiber.

As tending to cause deviation from the ideal standard we have already noted mechanical injury of the nerve before hardening and to this must be added delay in dissection after death.

In this connection some of the material received through the kindness of Dr. HARDESTY calls for special comment—comment which is made with the full recognition of the good fortune which brought the specimens into our hands and is merely intended to indicate how readily the nerves undergo slight alterations after death. Specimens 35-38 and 40-44 inclusive were given us by Dr. HARDESTY, the animals in all cases coming from the Zoölogical Garden in San Francisco.

Dr. HARDESTY writes as follows: ''In every case the animals from which I sent you bits of nerve were dead when they came into my hands. Most of them came to me within a few hours after death, and none had been dead more than twenty-four hours. In case of the monkeys, most died of tuberculosis, some of the other animals died of pneumonia, one by dysentery, one by accident and the bear from poison.''

On looking over our results on this material

Specimen	34,	Agouti
"	36,	Fox
"	38,	Wild-cat
"	43,	Ape

show excessively large sheaths, giving 160 fibers with an average of + 4%, while among the remainder of the mammals from San Francisco, namely the bear, Manila monkey, spider monkey, Rhesus and baboon the average is only +1.14%. We conclude from this that the nerves of the first group had suffered a slight post-mortem alteration before they could be fixed.

The deviations observed.—Table VI shows that the aver-age deviation for all the 1540 fibers is +0.45 %.

On determining the deviations separately for the Fish, Amphibia, Reptiles, Birds and Mammals we obtain the follow-ing results:

	Number of Fibers	Deviation
Fish	320	– 0.46%
Amphibia	250	– 0.87%
Reptiles	160	+ 1.70%
Birds	120	– 1.70%
Mammals	690	+ 1.40%

This tabulation serves to show that in no class do the de-viations rise very high, and that with the exception of the mammals, which have been commented on already, the aver-age deviation tends to diminish as the number of cases increases.

On further looking over the individual deviations, as shown in the original records, it appears that in 580 cases (or 37 % of 1540), they are more than 6% plus or minus—266 cases being minus and 314 plus. Thus the excessive deviations are rather evenly divided on either side of the average.

It follows from this that 63 % of the cases deviate only 6 % or less, or are within the anticipated error of observation.

From the foregoing it is concluded that despite the indi-vidual variations which may be often quite large, there is no tendency for the sheath to depart materially from the ideal standard, when this relation is determined by averaging the measurements obtained from groups of twenty or more fibers.

Figure illustrating variations in the thickness of the medul-lary sheath.—In order to give a meaning to the numbers that appear in the foregoing Table VI, the measurements applying to Specimens I, XI, XXII, XXIV, XXVIII, and XLV have been selected for illustration (see Fig. 1). This selection gives one specimen from each of the great classes below the mam-mals. In the case of each specimen, the diameter of the aver-age fiber is taken as a standard, and this is shown, enlarged one thousand diameters, (1) with a sheath having just half the area of the entire fiber (Ideal); (2) with the sheath determined from the
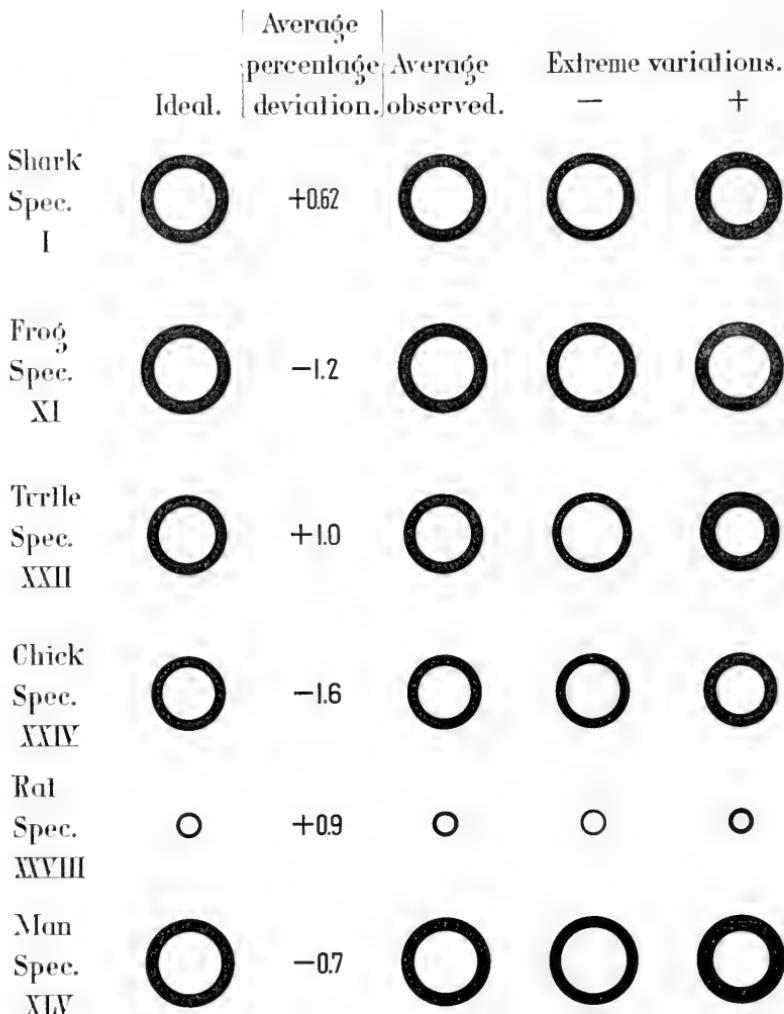
Figure 1

average of all the measurements (average observed) ; (3) with the smallest sheath observed in the series, and (4) with the largest sheath observed in the series (extreme variations).

By the study of Fig. 1, some notion of the range in the size of the sheath is obtained, but at the same time it must be remembered that these extreme cases as seen in (3) and (4) are exceptional, and that most of the deviations in the sheath are of decidedly less extent.

Conclusions.

The measurements in Table VI have been compared with one another in so far as they permitted the comparison of (1) nerves having different diameters ; (2) those afferent or efferent in function ; (3) taken from various parts of the body ; (4) in males and females ; (5) at different seasons ; (6) at different ages ; and (7) in animals active and those slow in their movements.

From such comparisons there is no indication that any of these conditions modify the relative development of the medullary sheath.

To make these statements with regard to area the basis for a statement with regard to the relative volumes of axis and sheath, is justified for the reason that the medullary sheath in the peripheral system is very nearly coextensive with the enclosed axis cylinder, and the short stretches at either end of the fiber would serve to give only a slight increase in the volume of the axis. Since in cross sections the sheath is on the average a trifle in excess of the axis, this difference would tend to make the similarity in volume even closer.

If the foregoing statements are well founded it should follow that the figures which represent cross sections of nerve fibers treated by the osmic acid method and which have been published in special articles or in text-books should accord with the results here given.

We have examined such figures as they appear in Ranvier ('78), Kupffer ('83), Gaskell ('85), Cajal ('99), Huber ('00), and find that when the conditions are observed of selecting only

those fibers which are nearly circular, in which the sheath is single and where there has been no increase in sheath from careless printing, the measurements show the same relations which we obtained on the specimens themselves.

We feel justified, therefore, in making the broad statement that in the peripheral nerves of vertebrates above the Cyclostomes, we have in general a one to one relationship existing between the nerve sheath and the axis, whether we compare the volumes of the two or measure their areas in the cross sections of osmic acid specimens. It is to be anticipated, however, that somewhere among the fish we shall find examples of less complete development of this sheath, thus bridging the gap between the condition here found and that represented by the nerves of Cyclostomi and Acrania which are without the medullary covering.

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ON THE NUMBER AND RELATIONS OF THE GANG-LION CELLS AND MEDULLATED NERVE FIBERS IN THE SPINAL NERVES OF FROGS OF DIFFERENT AGES.

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CONTENTS.

I. Introduction.

That the number of medullated nerve fibers in the spinal nerves increases during the growth of the animal toward maturity is generally accepted. Aside from the evident requirements of growth, the fact has been established on several occasions, at least for the frog and mammal, by direct enumerations of the fibers.

In two papers of some years ago the author ('99 and '00) undertook to determine the rate at which the increase of fibers takes place in the frog. It was then found (1) that the increase occurs more rapidly in younger specimens; (2) that in specimens of varying weights, counts of the fibers in transverse sections taken at intervals along the ventral root toward the spinal cord

and along both the dorsal root and the nerve trunk towards the spinal ganglion, showed a gradual increase of fibers at the average rate of nearly 2% per millimeter of length of the roots and of the trunk ; (3) in considering the VIth nerves alone of a series of 17 specimens ranging gradually in weight from 5 grams to 79 grams, it was found that in this one pair of spinal nerves there was for each gram of weight gained an average gain of 7.4 fibers in the two nerve roots and 10.4 in the trunk and dorsal branches.   As to the numerical relations of the fibers present on the proximal and distal sides of the spinal ganglia, there was always found (4) an appreciable excess of fibers in the sum of the trunk and dorsal branches as compared with the sum of the dorsal and ventral roots.   This "distal excess" was found to vary in the different spinal nerves, ranging from 7% to as much as 61% of the sum of the two roots.   It was found to be greater in those spinal nerves which have a relatively greater number of fibers in the dorsal branches, but showed neither a regular increase nor decrease with the increase in the size of the specimens.

BIRGE ('82) had previously counted the ventral root fibers of all the spinal nerves of one side of six frogs varying in weight from 1.5 to 111 grams and, assuming the fibers of the two sides approximately equal in number, his figures show an average total gain of 51 ventral root fibers for each gram gained in body weight.   HATAI ('02 and '03) has since determined the number of medullated fibers in the dorsal and ventral roots of three given spinal nerves of each of four white rats ranging in body weight from 10 to 264 grams.   He finds that the number of fibers in the roots of these three nerves is 2.7 times greater at maturity than in the 10 gram rat, and that the increase is more rapid in the younger animals.   BIRGE, though he did not take into consideration the dorsal branches, obtained noticeable distal excesses of fibers in the several nerves, and he was the first to attach significance to it.   GAULE and LEWIN ('96) investigating the sacral nerves of the rabbit, found an excess of fibers on the distal side of the spinal ganglion amounting to as much as 19%, and BÜHLER

('98) mentions a distal excess of 25% in the IXth spinal nerve of the frog.

An investigation of the numerical relations of the axones on the two sides of the spinal ganglion naturally suggests an inquiry as to the number of ganglion cells in it and the relation they bear to the numerical arrangements of the fibers. This paper is offered with the hope of contributing something (1) to the knowledge of the relations between the number of the nerve fibers in the dorsal roots and the number of ganglion cells in the spinal ganglia whence the fibers are supposed to arise ; (2) toward throwing further light upon the conditions determining the excess of fibers on the distal side of the spinal ganglion ; and (3) concerning the influence of growth upon the relative number of ganglion cells and the numerical relations of the fibers in the region of the ganglion.

The investigation was begun some time ago when the author was connected with the neurological laboratory of the University of Chicago. It has been allowed to rest on account of the difficulty in obtaining the material required. *Rana virescens* having been employed in the beginning of this and and the previous papers with which the results of this must be compared, it was thought advisable to continue with this species though it is apparently very rare in California. It finally became necessary that the material from the specimens of the sizes required to complete the work be sent from the laboratory in Chicago, and I desire to thank Professor DONALDSON and Dr. DUNN for their kindness and care in obtaining it for me.

Finally, let it be said that the author realizes that the results of an investigation of this kind are valueless unless obtained by most trustworthy procedure.

II. Material and technique.

Only three of the spinal nerves of each frog are dealt with. These are the Vth, VIth, and IXth of each of seven frogs varying in weight from 10.4 to 63.4 grams. The Vth was chosen as a typical thoracic nerve and because, being near the lumbar region, its dorsal and ventral roots are long enough to render manipulation less difficult. The VIth nerve in many respects is similar to the thoracic nerves anterior to it,

but at the same time it is often larger than the Vth and in some re-
spects resembles the VIIth which belongs almost entirely to the lum-
bar distribution. Morever, the VIth was employed in a previous in-
vestigation ('oo) and is included in this in order to accumulate data con-
cerning it. The IXth nerve was chosen because it is one of the largest
spinal nerves in the frog, and differs from the Vth and VIth in that all
the fibers of its trunk are contributed to the lumbar plexus. These three
nerves alone are considered, it being assumed that whatever conditions
found true for these are approximately true for the remaining spinal
nerves. To enumerate the ganglion cells and the nerve fibers in the
dorsal and ventral roots and the trunks of the entire ten spinal nerves
would have been so arduous a task that the additional information
probably to be obtained by such was considered a reward scarcely
sufficient for the ordeal.

To obtain a series ranging as gradually and as widely as possible,
each specimen was chosen with reference to its body weight. The
smallest specimen of *Rana virescens* obtained for this observation had a
body weight of 10.4 grams. Smaller specimens may be obtained at
certain seasons of the year just after the transition from the tadpole
stage. The largest specimen of the series weighed 63.4 grams and
was, of course, female, since the males seldom exceed 50 grams while
the females have been known to attain a body weight of 80 grams
with the ovaries removed.

In each case the animal was chloroformed in the usual way and,
if female, the ovaries were removed. It was then weighed and its
body weight and sex recorded. The procedure in dissecting, fixing,
imbedding, sectioning, etc., was much the same as that followed in the
previous investigation and it is there given in detail. The spinal cord
was laid bare from the ventral side, the spinal ganglia and dorsal
branches carefully exposed and dissected free with the aid of the dis-
secting microscope. Avoiding pulling and stretching, the dorsal and
ventral roots were clipped with fine scissors close up to the spinal cord
and the nerve trunk near its junction with the ramus communicans.
Then the ganglion with the roots and portion of the nerve trunk at-
tached was laid on a small piece of card-board. There the roots were
arranged straight and parallel with each other, and the dorsal branches
straightened out parallel with the nerve trunk in order to obtain trans-
verse sections of the two with the same stroke of the knife. In doing
this, careful use of the dissecting lens was always advisable lest some
of the smaller of the dorsal branches should be overlooked and should
remain tangled or doubled back upon themselves, and thus in the sec-

tions occasion a double counting of the fibers contained in them. In each case the strip of card-board with the specimen arranged upon it was placed into a vial containing 1% osmic acid and bearing a label stating the date, the weight and sex of the animal, the number of the spinal nerve, and whether taken from the right or left side. After being subjected to the action of the fixing agent for 15 or 20 minutes, the parts become stiffened sufficiently to maintain their arranged relations and may be gently lifted from the card-board that the fluid may penetrate more freely from all sides. The larger nerves were always removed into the fluid. After 12 to 24 hours in osmic acid, the specimen was washed about 12 hours in water frequently changed, and then transferred to 70% alcohol. While washing, an outline sketch of the specimen was made for the purpose of orientation.

Each specimen was embedded in paraffin separately in a small paper box on the side of which was copied the label on the vial in which it was fixed, washed, dehydrated, etc. Transverse sections of the two nerve roots of the trunk and dorsal branches were made of about 4 μ in thickness, and those from the required localities were mounted serially. The sections of the nerve roots were taken from about midway their length, while those from the trunk and dorsal branches were taken close up to the peripheral side of the spinal ganglion, yet far enough away to avoid any portion of the ganglion itself being involved. Separate slides were devoted to each of the localities required, and the locality mentioned in their labelling. On approaching the ganglion, from whichever side the sectioning was begun, the thickness of the sections was changed. All sections involving the ganglion were made 9 μ thick and special attention was given to mounting them serially.

For counting the nerve fibers the photographic method, devised in the neurological laboratory of the University of Chicago ('99) was employed for every section except an occasional very small twig of the dorsal branches. The mounted sections from a given locality were first carefully looked over with the compound microscope, and one suitable for photographing was picked out, that is, a perfect section and one which high power showed to be flat and evenly adhering to the surface of the slide. Under low power this section was marked by a ring of ink on the cover glass. The photographs were made with the aid of the Zeiss projection apparatus. The magnification employed was from 300 to 500 diameters, varying according to the size of the section None of the sections in this investigation when sufficiently magnified were too large to get on a single plate of the

largest size the apparatus accommodates. Since only medullated nerve fibers were to be counted and since, after osmic acid, these are indicated by the dense black deposit of the reduced oxide of osmium in their medullary sheaths, it was desirable to get photographs giving as much contrast as possible. For this reason, some form of the photographic plates used in "process work" was usually employed. These also allow considerable latitude in the exposure and always give strong negatives. With strong negatives, a good quality of blue print paper gives excellent results for the purpose required, and this was used throughout because of the simplicity of its manipulation as well as its inexpensiveness.

In making the counts of the fibers in a section, the photograph of the section was pinned out upon a soft pine board and the identical section itself placed under the compound microscope and subjected to higher magnification than that under which it had been photographed. After a few minutes study, any field in the photograph could be identified in the microscope. Then with a sharp pointed pencil, the photograph was divided into fields of about one inch square or less in area, the lines of division passing among and between the fibers instead of across them. The actual enumeration was done with an automatic tallying register, to the thumb-press of which had been fixed a needle holder. Each fiber in one of the outlined fields was punctured by the needle and all doubtful cases were settled by reference to the original under the microscope. The counting of one field was finished before beginning another. The counting apparatus, its use and the trustworthiness of the results obtained with it, are discussed in detail in the paper cited above. The method has since been used with little modification (DUNN '00, HATAI '02, INGBERT '03) and the results obtained have been uniformly considered satisfactory. The method has the advantage of being largely mechanical and eliminating as far as possible the psychological sources of error which are most to be feared in investigations of this kind.

It was not deemed necessary to photograph certain of the small divisions of the dorsal branches. Such as were small enough to bear a magnification of 700 diameters and still not occupy the field of the microscope, were counted by a modification of the more commonly used net-micrometer method. The procedure followed is fully described in the author's paper of 1900. By means of the projection of the squares of the micrometer and the completion of the count before the result is known, it is held that all errors of auto-suggestion are avoided.

In counting the ganglion cells an application of the net method had to be used exclusively. Here all the sections involving the ganglion had to be gone over and photography was practically out of the question. Therefore, the problem had to be approached in another way. It was first determined that but few of even the very smallest of the spinal ganglion cells have a diameter of less than 9 μ, and further that 9 μ sections were thin enough to allow the light to pass through sufficiently to distinguish the intervening structures of the cell. For this reason 9 μ was chosen as a convenient thickness. On the other hand, however, some of the largest cells of the ganglia may extend through as many as seven consecutive sections of this thickness. To obviate the danger of double counting, a procedure was adopted throughout, which I think was first described by GAULE and LEWIN ('96) in their enumerations of the spinal ganglion cells of the rabbit. This consisted in counting only the nucleoli in the sections. As with them, the question of course arose as to the danger of double counting because of the existence of double nucleoli. In counting the cells in several of the ganglia here dealt with, I kept a record of the double nucleoli appearing in the sections and found that two nucleoli occurred in the same cell at an average of about 5 cells in 1000 or at the rate of about one-fifth of 1 %. Cells in which they were observed were usually among the smaller cells of the ganglia. They, of course, were not counted twice. Remembering that these double nucleoli were seen in sections of 9 μ, and that double nucleoli in a nucleus are never separated as much as 9 μ from each other, and further, that certainly not more than half of such cases existing have their nucleoli separated in the plane perpendicular to the plane of the knife in sectioning so that the knife may pass between them, it is therefore evident that the number of cells counted twice because of double nucleoli is probably less than one-fifth of 1 %. The proabilities of double counting due to nuclei being cut in half by the knife and thus counted in the two sections, are also such as need only be considered in questions of the most absolute accuracy. In exceedingly few cases did appearances and comparison of the consecutive sections indicate this had happened. None of the conclusions drawn in this paper would be materially affected by an acknowledged error of one-fifth of 1 %.

The number of cells counted in each section was recorded separately and not till all the sections of a ganglion had been counted were these numbers added to obtain the total number of cells in the ganglion. The larger ganglia often involved as many as 125 sections. In no case was the relation between the number of ganglion cells and the

number of fibers in the dorsal root computed till all the nerves of a specimen had been completed.

The serial sections were always followed for some distance on either side of the spinal ganglion proper in search of out-lying ganglion cells. In one case these comprised the appreciable total of 31 cells. In most cases the number was very small. In some cases they were more abundant in the beginning of the dorsal root, in others there were more in the trunk. In the Vth and VIth nerves, the mass of the ganglion shows a tendency to protrude distally along the dorsal branches instead of along the trunk. This is due to the probable fact that most of the fibers of the dorsal branches are cutaneous in their distribution.

III.   *General results of the enumeration.*

Following the procedure indicated above, the Vth, VIth and IXth spinal nerves were investigated from 7 frogs varying in body weight from 7 to 63.4 grams. The number of ganglion cells in the spinal ganglia of each nerve was determined and the number of nerve fibers present in the dorsal root, the ventral root and the number in the dorsal branches and in the trunk taken close up to the peripheral border of the spinal ganglion but beyond the region of outlying ganglion cells. The general results of these enumerations are given in the following tabulated form :

TABLE I.   Showing in their respective columns the number of fibers in the dorsal roots, the number of cells in the spinal ganglia, the number of fibers in the ventral roots and in the trunks and dorsal branches of the Vth, VIth, and IXth spinal nerves of 7 frogs varying in body weight as indicated in the first column. The ratios of the ganglion cells to the dorsal root fibers (col. C) are obtained by dividing the numbers in col. B by those in col. A. The figures in col. E result from subtracting those in col. F (fibers in the ventral roots) from those in col. G, and the ratios in col. D are obtained by dividing those in col. B by the respective numbers in col. E. The sums of fibers in the two nerve roots and the sums in the trunk and dorsal branches of each nerve are entered (col's. K and G) for purposes of comparison, but especially that the correctness of the amount of the excess of fibers on the distal side of the spinal ganglion (col. I) may be determined. The percentage of the "distal excess" (col. J) results from dividing the amount of the distal excess (col. I) by the sum of fibers in the dorsal and ventral roots (col. K). The ratios comparing the number of fibers in the ventral roots with the number of fibers in the dorsal roots (col. L) are obtained by dividing the numbers in col. A by those in col. F.

TABLE I.

IXth NERVE

Measurement								Average
Body weight in grams	7.0	10.4	25.3	33.7	47.4	61.8	63.4	
A. No. of fibers in the dorsal root	204	257	217	235	279	338	293	
B. No. of cells in the spinal ganglion	718	871	674	574	788	1257	1012	
C. No. of cells per fiber in dorsal root	3.5	3.4	3.1	2.4	2.8	3.7	3.5	*3.2*
D. No. of cells per fiber in trunk and dorsal branches less the ventral root	2.5	2.4	2.0	1.8	1.7	2.1	2.2	*2.1*
E. No. fibers in trunk and dorsal branches less the ventral root	280	355	338	335	434	611	468	
F. No. of fibers in the ventral root	71	100	94	127	193	131	135	
G. Sum of fibers in the trunk and dorsal branches	351	455	432	462	627	742	603	
H. No. of fibers in the dorsal branches	211	232	232	141	307	307	310	
I. "Distal excess."	76	98	121	100	155	173	175	*143*
J. Percentage of distal excess	27.6	27.4	28.9	27.6	32.8	58.2	40.8	*37.8*
K. Sum of fibers in dorsal and ventral roots	275	357	311	362	472	469	428	
L. Ratio of fibers in the ventral root to fibers in dorsal root	1:2.9	2.6	2.3	1.8	2.6	2.2	2.3	

VIth NERVE

Measurement								Average
Body weight in grams	7.0	10.4	25.3	33.7	47.4	61.8	63.4	
A. No. of fibers in the dorsal root	193	235	239	273	341	311	357	
B. No. of cells in the spinal ganglion	545	792	684	734	842	1075	1151	
C. No. of cells per fiber in dorsal root	2.8	3.3	3.3	2.5	2.7	3.5	3.3	*3.0*
D. No. of cells per fiber in trunk and dorsal branches less the ventral root	2.0	2.7	2.0	1.6	1.5	2.5	2.0	*2.1*
E. No. fibers in trunk and dorsal branches less the ventral root	168	290	306	472	557	436	575	
F. No. of fibers in the ventral root	113	143	108	133	278	196	212	
G. Sum of fibers in the trunk and dorsal branches	381	433	414	605	835	632	787	
H. No. of fibers in the dorsal branches	249	197	204	148	276	380	378	
I. "Distal excess."	75	55	67	199	216	125	218	*136*
J. Percentage of distal excess	24.5	13.2	19.6	49.0	34.8	24.7	38.3	*29.2*
K. Sum of fibers in dorsal and ventral roots	306	378	347	406	619	507	569	
L. Ratio of fibers in the ventral root to fibers in dorsal root	1.7	1.6	2.1	1.2	1.6	1.7	1.7	

Vth NERVE

Measurement								Average
Body weight in grams	7.0	10.4	25.3	33.7	47.4	61.8	63.4	
A. No. of fibers in the dorsal root	1491	1231	1211	1808	1313	1645	1491	
B. No. of cells in the spinal ganglion	3842	4581	3104	4881	3571	4996	4608	
C. No. of cells per fiber in dorsal root	2.6	3.7	2.6	2.7	2.6	3.0	3.1	*2.9*
D. No. of cells per fiber in trunk and dorsal branches less the ventral root	2.4	3.4	2.4	2.5	2.3	2.7	2.6	*2.6*
E. No. fibers in trunk and dorsal branches less the ventral root	1612	1361	1316	1982	1528	1828	1713	
F. No. of fibers in the ventral root	931	719	741	1156	1176	1182	936	
G. Sum of fibers in the trunk and dorsal branches	2543	2080	2057	3138	2704	3010	2649	
H. No. of fibers in the dorsal branches	371	279	212	335	364	293	269	
I. "Distal excess."	121	130	105	174	215	183	222	*164*
J. Percentage of distal excess	5.0	6.6	5.9	5.9	8.6	6.7	9.1	*6.8*
K. Sum of fibers in dorsal and ventral roots	2422	1950	1952	2964	2489	2827	2427	
L. Ratio of fibers in the ventral root to fibers in dorsal root	1.6	1.7	1.6	1.6	1.1	1.4	1.6	1.5

In this table the results for each of the three spinal nerves involved are grouped in the order of the body weights of the respective animals employed in order that the figures obtained for the different representatives of a given spinal nerve may be compared more readily with each other as well as with those of the other spinal nerves.

In the first place, it is apparent as far as the three nerves presented are concerned that neither the number of fibers nor the number of ganglion cells in a given nerve of a specimen is regularly dependent upon the body weight of the specimen. This is perhaps entirely due to a fact noted previously ('99) when was given a more detailed description of the macroscopic features of the different spinal nerves of the frog, viz. : that when the spinal neves of the different specimens are are compared, the relative proportion of fibers distributed to a given nerve is by no means fixed. The variations in proportional size are more frequent and marked in the VIIth, VIIIth, and IXth nerves. In the general arrangement, the VIth is much smaller than the VIIth, and the VIIIth (the largest of the lumbar nerves) is considerably larger than the IXth; but occasionally the relative size of these nerves can be observed even with the unaided eye as decidedly different in different frogs and sometimes, indeed, on the two sides of the same frog. The variations are most frequent in the VIIIth and IXth nerves, the apparent condition being that a portion of the bulk usually possessed by the VIIIth may be contributed to the IXth instead, for when the proportional size of the IXth is greater than usual, that of the VIIIth is less. In the case of the frog weighing 7.0 grams, recorded in the table, it was noticed at the time of its dissection that the IXth nerves of both sides were appreciably larger than the VIIIth nerves. It was included, however, because at the time I was unable to obtain another specimen of *Rana virescens* as small as this. Some of the other discrepancies in the increase in the number of fibers accompanying the increase in body weight are without doubt due to similar variations. To determine the real rate of the increase, all the spinal nerves of the different specimens should of course be included in the

·counting. For the three nerves involved here, this table shows that, though the variation is not very regular, the larger specimens give the larger numbers. In some of the succeeding tables where the numbers are summed up and arranged according to the body weight, this fact is more evident. It is one of the features for which Table III is especially constructed.

In the last column of Table I the number of fibers in the ventral roots are compared with the number in the dorsal roots. The proportional relations are expressed in the form of ratios. It is seen (1) that in every case the dorsal root fibers exceed those in the ventral root; (2) that in the Vth nerve this excess is greater than in the VIth while in the VIth it is greater than in the IXth, and (3) that the ratios do not vary with the variations in body weight. In five cases the dorsal root fibers of the Vth nerve are more than twice the number in the ventral root. In the VIth there are but two such cases and in the IXth there are none, but in the latter the relation is much more uniform than in either of the other two. The average ratios, computed for each of the nerves, show more readily the differences between the excesses of dorsal root fibers in the Vth and VIth nerves and the excesses in the IXth. Very similar ratios may be obtained from the numbers pertaining to these three nerves determined in the previous investigation ('99). Both the IXth nerves recorded there show the dorsal roots as having 1.5 times as many fibers as the ventral roots, thus agreeing with the average found here. There it was shown that of all the spinal nerves of the frog, only the Ist, IIIth and Xth possess an excess of fibers in their ventral roots. That the excess of dorsal root fibers is greater in the VIth and especially in the Vth than in the IXth nerve coincides with the fact that a greater proportion of their fibers are contributed to the skin than is the case in the IXth. They are much smaller than the IXth and in many cases the number of fibers in their dorsal branches exceeds the number in the nerve trunk (see Table III), and so great a proportion of fibers in the dorsal branches are sensory that the peripheral border of the spinal ganglion may nearly

always be seen to protrude along the dorral branches instead of upon the trunk.

For the entire 21 nerves included here the general average ratio of medullated fibers in the ventral roots to those in the dorsal roots is 1:1.8.   BIRGE's work with *Rana esculenta* ('82) gives the similar ratios of 1:1.7 and 1:1.8, and the author's previous work gives for the same three nerves an average ratio of 1:1.6, and for the VIth nerve alone of 19 specimens, a ratio of 1:1.8.   This similarity in the proportion of fibers in the motor and sensory roots indicates that whatever other changes may take place, a more or less fixed numerical relation is maintained between the two.

For all of the spinal nerves of one side of the frog, BIRGE's figures give a ratio of ventral to dorsal root fibers of 1:1.2.   HATAI ('02), investigating three of the spinal nerves of the white rat, finds in every case more fibers in the dorsal than in the ventral root.   The excesses varied from 2 to 2.9 times the ventral root fibers and gave an average ratio of 1:2.5.   INGBERT ('04) has recently completed the enumeration of the fibers in the dorsal and ventral roots of all the spinal nerves of one side of an adult man and it is interesting to note that the ratio found by him is considerably higher than that found in either the frog or the rat.   He finds in the sums of all the roots of one side that the ventral root fibers are exceeded by those in the dorsal roots in the ratio of 1:3.2.   In comparing the different regions of the spinal cord, he further shows that the excess of dorsal root fibers runs appreciably higher in most of the cervical and lumbo-sacral nerves than in any of the thoracic region.   HATAI's figures indicate this to be true for the white rat also, and to some extent the figures available show it true for the frog.   It is explained as entailed in the requirements for the inervation of the relatively greater skin area of the upper and lower limbs.

HATAI, dealing with rats of different ages, found further that the excess of dorsal root fibers was greater in the young than in the adult, and thus with reason claims that the ventral root fibers increase in number more rapidly between the periods of medullation and maturity than do the dorsal root fibers.   If

the specimens of Table I be separated into two groups, letting the first three comprise a group of younger against the last four as a group of older specimens, and the sums of their root fibers compared, it will be found in each of the three nerves that the excess of dorsal root fibers over those of the ventral root is greater in the younger than in the older specimens. The differences in the ratios in favor of the younger, however, are not so marked as HATAI finds in the white rat. This is perhaps due to the fact that the frog has a relatively longer period of general growth than the white rat and, while its ventral root fibers do increase more rapidly than those in the dorsal root, the whole process of growth is slower. This point will be approached from another direction in the discussion of Table IV.

In every case Table I shows that there is a considerable excess of fibers in the sum of the trunk and dorsal branches above the sum of fibers in the ventral and dorsal roots (col. I). As compared with the sum of fibers on the central side of the spinal ganglion, this excess will be referred to as the ''distal excess.'' It will be considered in more detail under a separate heading and with a differently arranged table, but since Table I better allows a comparison of the three nerves with each other it may be noted here (1) that in each of three nerves the distal excess shows a decided, though irregular, increase with the increase in body weight; (2) that, though it is evidently dependent to a certain extent upon the amount of the dorsal branches, in neither of the nerves does it show marked coincident variation with the number of fibers in the dorsal branches (col. H); (3) that while the percentage of the distal excess (col. J) varies to a considerable exent with the proportional relation of the dorsal branches to the nerve trunk, the actual amount of the distal excess does not do so; (4) the average amount of the distal excess is approximately similar in each of the three nerves and the same is true for the average amount of the dorsal branches in each of the nerves ; (5) the percentage of the distal excess ranges somewhat higher in the Vth than in the VIth nerve and is much higher in both than it is in the IXth nerve.

*IV.   The number of spinal ganglion cells and their relation to·
the number of nerve fibers connected with the ganglion.*

It is seen in column A and B, Table I, that the numbers
of ganglion cells vary much as do the numbers of fibers in the
dorsal roots.   This is to be expected.   But it is also seen that
there are many more cell-bodies in the ganglia than there are
fibers in the corresponding dorsal roots.   The counts show a gen-
eral average of three times as many cells in the ganglia as fibers
in the dorsal roots.   The averages obtained for each of the three
nerves are quite similar, being somewhat greater for the Vth
and VIth than for the IXth.   The ratios (col. C) show no tend-
ency in either of the nerves to vary with the weight of the
animal.

This excess of cells in the spinal ganglion above the num-
ber of fibers in the dorsal root agrees fairly well with the re-
sults obtained by HODGE ('88) whose paper, as far as I am
aware, is the only other dealing with an American species of
frog.   He counted the ganglion cells and dorsal root fibers in
the VIIth, VIIIth and IXth nerves of a single specimen and ob-
tained ratios of cells to fibers of 1:2.5, 1:2.9, 1:3.3 respectively,
giving an average of 2.9 cells per each dorsal root fiber.   BÜHLER
('98) investigating the spinal ganglia of *Rana esculenta*, counted
the cells and dorsal root fibers of one of the IXth nerves·of one
specimen and found 5 cells per fiber.   This is considerably
higher than any of my results.   It may have been peculiar to
the one nerve investigated or it may be peculiar to the species.
For the mammals, GAULE and LEWIN ('96) found in the
XXXIIth nerve of the rabbit 6.4 spinal ganglion cells per fiber
in the dorsal root of the nerve, and HATAI ('02) for three of the
spinal nerves of each of four white rats of different ages, ob-
tained excesses of cells ranging from 11.5 in the younger down
to 2.7 per fiber in the adult, always finding twice as many cells
as dorsal root fibers.   On the other hand, FREUD ('78) working
with the less perfect technique of his time, concluded that in
Petromyzon the number of spinal ganglion cells were equal to
the number of dorsal root fibers.

The distal excess realized, it might be natural to suppose that many of these extra cells are such as send processes toward the periphery without sending corresponding processes into the dorsal root. After subtracting the motor or ventral root fibers (col. F) from the sum found on the peripheral side of the ganglion (col. G), it is seen that there is still an average of more than twice as many cells as there are fibers which can possibly be considered as arising in the spinal ganglia. These ratios (col. D) vary quite closely with the ratios having to do with dorsal root fibers (col. C). By comparing columns C and D it appears that there is in the Vth and VIth nerves an average of about one cell less per distal fiber than there were cells per fiber in the dorsal roots, while in the IXth nerves this average is only 0.3 cells less. The Vth and VIth are the nerves which have relatively the larger amount of distal excess and absolutely the larger percentage of distal excess.

Many of these extra cells are allotted to the category of the "DOGIEL spinal ganglion cell of Type II." However, none of the descriptions of this type indicate that they are sufficiently abundant in the ganglia to account for more than a very small proportion of the excesses of cells found there. A larger proportion of these extra cells belong probably to the anaxonic type of neurone, latent cells which have not yet developed processes. BÜHLER and HATAI suggest that this type consists among the smallest cells of the ganglia. In the nerves of the frog here investigated, the proportion of small to large cells is greater in the ganglia of the Vth and VIth nerve than it is in the IXth. This, however, is thought explainable on other grounds.

That the excess of cells above the number of dorsal root fibers is greater than the excess above the fibers on the distal side of the ganglion is no doubt due to some extent to certain of the so-called multipolar cells described in the spinal ganglia of various animals by KÖLLIKER ('93), LENHOSSÉK ('94), SPIRLAS ('96), DOGIEL ('97), CAJAL and OLORIZ ('98) and others. DOGIEL thinks that some of these may be modifications of his cell of Type II. Others are thought to be of the character of

sympathetic neurones and to send processes toward the periphery without sending a corresdonding process into the dorsal root. Another cause for the excess of cells above the fibers being less on the distal side of the spinal ganglion, is due to the bifurcation of fibers on the distal side. Both this and the multipolar cells of the character just mentioned contribute to the formation of the excess of fibers on the distal side of the ganglion and both will be considered in the discussion of the "distal excess."

On neither side of the spinal ganglion does the number of cells per each fiber supposedly connected with the ganglion show a regular decrease with the increase in the body weight of the specimens. Such a decrease might be expected with the usual conception that the number of ganglion cells becomes fixed at quite an early period in the growth of the animal, but my counts for neither of the three spinal nerves here represented show such with any regularity. HATAI ('02) found in the rat an appreciable decrease in the value of the ratios of cells to dorsal root fibers as the animal reached maturity. Either in this respect the processes of growth in the frog are again different, or the process is so slow in the frog as to require the investigation of a greater number of nerves of a greater number of individuals. Could the cells be counted at different periods of the growth of the same frog, the result might be different, for it must be remembered that each set of figures in Table I but represents the conditions in 'the nervous system of a different individual at a certain time.

The growth relations are shown in another way in Table II which is constructed with reference to the body weights instead of grouping with reference to the number of the spinal nerve as in the table above. Such results as may be brought out by arranging the frogs into two groups, one containing the larger and the other the smaller frogs, and summating the numbers in each will be presented later.

TABLE II.

Body weight in grams.	Spinal nerve.	A / B No. of cells in spinal ganglion of each nerve.	C Sums of cells in spinal ganglia.	D Sums of fibers in the dorsal roots.	E No. of cells per fiber in dorsal roots.	F No. of cells per fiber in trunks and dorsal branches less ventral roots.	G Sums of fibers in trunks and dorsal branches less ventral roots.	H No. of fibers in trunk and dorsal branches less ventral root.	I No. of fibers in dorsal root of each nerve.
7.0	5th	718						280	204
	6th	545						168	193
	9th	3842	5105	1888	2.7	2.5	2060	1612	1491
10.4	5th	871						355	257
	6th	792						290	235
	9th	4581	6244	1723	3.6	3.1	2006	1361	1231
25.3	5th	674						338	217
	6th	684						306	239
	9th	3104	4462	1667	2.7	2.2	1960	1316	1211
33.7	5th	574						335	235
	6th	734						472	273
	9th	4881	6189	2316	2.7	2.2	2789	1982	1808
47.4	5th	788						434	279
	6th	842						557	341
	9th	3571	5201	1933	2.7	2.1	2519	1528	1313
61.8	5th	1257						611	338
	6th	1075						436	311
	9th	4996	7328	2294	3.2	2.6	2875	1828	1645
63.4	5th	1012						468	273
	6th	1151						575	357
	9th	4608	6771	2141	3.2	2.5	2756	1713	1491
	Averages				3.0	2.4			

TABLE II. Allowing a comparison of the number of cells found in the spinal ganglia (col. B), the number of fibers in the dorsal roots (col. I) and of the number of fibers found in the trunks and dorsal branches (col. H) of the Vth, VIth and IXth spinal nerves of each specimen. The different specimens are entered in the order of their body weight. In columns C, D and G the sums of the ganglion cells, the sums of the dorsal root fibers and the sums of the fibers in the trunks and dorsal branches found in the three nerves of each frog may be compared with each other and, reading downward, the sums in each column may be compared with reference to the increase in body weight. Column E, obtained by dividing col. C by col. D, presents the ratios of ganglion cells to dorsal root fibers in the three nerves combined of each specimen and likewise col. F shows the number of cells in the combined ganglia per each fiber in the total of the trunks and dorsal branches less the ventral root fibers of each specimen.

Table II shows (col. E) that when the numbers found in the three nerves of each specimen are combined, the ratios of the sum of the ganglion cells to the sum of the dorsal root fibers show even a less tendency to decrease with increase in the body weight than is manifested when each of the nerves is considered separately as in the previous table. Indeed, two of the three cases in which the sum ratio is highest are in the two largest specimens. · The sum ratios of cells to fibers on the distal side of the ganglion (col. F) follow so closely the variations of the ratios dealing with dorsal root fibers that whatever is true for the one is practically true for the other.

By comparing columns E and F it is seen that in the sums of the cells and fibers in the three nerves of the several frogs, the number of cells per fiber on the distal side of the ganglion is only from 0.2 to 0.7 of a cell less than on the central side. The cases in which the difference is greatest are in the largest specimens. The average difference is 0.6. In was seen in Table I that when the Vth nerves alone are considered this difference averages 1.1 cells, being less in the VIth and much less in the IXth nerves.

In columns B and H, Table II, better than Table I, is also illustrated the fact that the relative number of cells and fibers apportioned to a given nerve varies greatly. To the unaided eye the Vth nerve usually appears smaller than the VIth, but in three of the seven frogs here it contains appreciably more cells and fibers than the VIth. This variation from the usual proportion is more frequent in the IXth nerve but its variation is less manifest here because of the absence of figures for the nerves adjacent to it. The relatively large sums for the 7 gram frog are due to its having comparatively a much larger IXth nerve than usual for its weight. Also the IXth in the 25 gram frog seems to have been small. In column I it is seen that the numbers of dorsal root fibers vary much as the ganglion cells and as the fibers on the distal side of the ganglion.

V. Further observations on the conditions determining the excess of fibers on the distal side of the spinal ganglion.

The distal excess was described in the previous papers and some attention was given to probable arrangements of the fibers in producing it. It was shown in a series involving all the spinal nerves of one side of a frog, (1) that of all the nerves, those which in proportion to their trunks have the largest number of fibers in their dorsal branches have also the highest percentage of distal excess; (2) that in some cases the amount of the distal excess may even exceed the number of fibers in the dorsal branches; (3) that while in a given nerve (VIth, consid-from a series of 19 frogs) the increase in weight is not accompanied by a regular increase in the value of the distal excess in this nerve, yet when the results are grouped for the small and large separately, the distal excess for this nerve shows a decided increase with the gain in weight. It was further suggested that the distal excess is due (1) to the medullated fibers from the sympathetic system which terminate in the spinal ganglion, (2) to cells in the ganglion which send processes toward the periphery but not into the dorsal root, (3) to the bifurcation of the peripheral prolongation of the spinal ganglion neurone of Type I and (4) to the bifurcation of ventral root fibers in the region of the spinal ganglion.

The observations as to the variations and causes of the distal excess made in these papers, one using the several nerves from one specimen and the other the one nerve from several specimens, should gain significance if further based upon the findings in several nerves from each of several specimens. Table III is constructed with special reference to the distal excess and is given as indicating further some of the number relations involving it The table is compiled from the numbers in Tables I and II and represents some relations not brought out in the previous work.

Attention is called to the following relations as shown in Table III.

1. When the different nerves of each specimen are considered indidually, the number of fibers in the nerve trunk (col. A) and those in the dorsal branches (col. B) do not show a regular increase with the increase in body weight. The same is true for the sums of these fibers in the three nerves of each specimen (col's. C and L). However, though the increase is not a regular one, the larger specimens have appreciably more fibers than the smaller ones. The same statements apply to the numbers of fibers in the dorsal and ventral roots (col's. D and E).

2. It is evident here (col's. C and D), and especially so when computed (see Table IV), that in the dorsal and ventral roots the increase of fibers with the increase in weight is not so great as in the trunks and dorsal branches. In other words, the fibers on the side of the distal excess increase more rapidly than on the central side of the spinal ganglion.

3. While the amount of the distal excess in each nerve (col. F) varies so greatly that its increase with the body weight is not very evident, yet when the sums of the distal excesses in each set of nerves are considered (col. G) there is manifest a decided and much more regular increase.

4. The most marked increase in the sums of the distal excess appears in this series between the weights of 25 and 61 grams. Between 25 and 33 grams the increase amounts to 27 % and in passing from 33 to 47 grams the increase amounts to 23 %, while the average increase from from one specimen to the

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TABLE III. Giving number relations involving the distal excess. The various columns are either rearranged or derived from the columns of Tables I and II. The sums in columns C, D and G result from adding in adjacent columns the numbers found respectively in the three nerves of each specimen. The percentages in col. J result from dividing the sums in col. G by the respective sums in col. D of Table II; the percentages in col. K from dividing col. G by the respective sums of ventral root fibers in col. C of Table IV. The sums in column P are obtained by substracting col. D of Table II from col. C of that table and the ratios in the last column result from dividing the numbers in col. P of this table by the sums in col. G. As indicated in the headings, all the other columns set in heavier type are derived from columns accompanying them in this table. The percentages are reduced to one decimal figure and the ratios are given in round numbers.

TABLE III.

		63.4	61.8	47.4	33.7	25.3	10.4	7.0
	Body weight in grams.							
	Spinal nerve.	6th 9th / 5th 6th 9th	5th 6th 9th	5th 6th 9th	6th 9th	5th 6th 9th	6th 9th	6th 9th
A	No. of fibers in trunk.	295, 416, 2356	435, 254, 2646	455, 320, 2369	321, 2747	200, 266, 1946, 1903	223, 229, 2331	140, 184
B	No. of fibers in dorsal branches.	310, 371, 293	307, 378, 364	307, 380, 335	391, 276, 335	232, 148, 154, 141	232, 204, 134	211, 197, 212
C	Sums of fibers in trunks and dorsal branches.	4039	4384	4166	4205	2903	2968	3275
D	Sums of fibers in dorsal and ventral roots.	3424	3803	5380	3732	2610	2685	3003
E	No. of fibers in dorsal and ventral roots.	2427, 569, 428, 2827	507, 469	2489, 619, 472	2964, 406, 362	311, 347, 1952, 357	378, 311, 2422	275, 306, 2422
F	The distal excess in each nerve.	222, 218, 175, 183	125, 273	215, 216, 155	174, 199, 100, 105	67, 121, 130, 55	98, 121	76, 75, 121
G	Sums of distal excess.	**815**	**581**	**586**	**473**	**293**	**283**	**272**
H	% of distal excess in each nerve.	9.1, 38.3, 40.8, 6.7	24.7, 58.2	8.6, 32.8, 34.8	5.9, 49.0, 27.6	5.9, 19.6, 28.9, 6.6	13.2, 27.4	27.6, 24.5, 5.0
I	% of sums of distal excess based on sums of roots.	**18.0**	**15.3**	**16.4**	**12.7**	**11.2**	**10.6**	**9.0**
J	% relations of sums of distal excess to sums of dorsal root fibers.	**28.7**	**25.3**	**30.3**	**20.4**	**17.6**	**16.4**	**14.4**
K	% relations of sums of distal excess to sums of ventral root fibers.	**47.9**	**38.5**	**35.5**	**33.4**	**31.1**	**29.4**	**24.4**
L	Sums of fibers in dorsal branches.	**974**	**1049**	**1022**	**808**	**534**	**570**	**620**
M	% relations of sums of distal excess to sums of dorsal branches.	**63.1**	**55.4**	**57.3**	**58.5**	**54.9**	**49.6**	**43.9**
N	% relations of sums of distal excess to sums of trunks & dor. branches.	**15.2**	**13.3**	**14.1**	**11.2**	**10.1**	**9.5**	**8.3**
O	% relations of sums of dorsal branches to sums of trunks & dor. branches	**24.1**	**23.9**	**24.5**	**19.2**	**18.4**	**19.2**	**18.9**
P	Sums of ganglion cells less sums of dorsal root fibers.	4630	5034	3268	3873	2795	4521	3217
Q	Ratios of sums of distal excess to sums of ganglion cells less sums of dorsal root fibers.	**8**	**9**	**6**	**8**	**10**	**16**	**1:12**

next in series is only about 13%. The first two and last two specimens differ less in weight than the others. The 47 gram frog was a male and the next in series, weighing 61 grams, was female. The distal excess in the two is about the same and the 63 gram frog, also female, shows an increase above the 47 gram male of only about 4%. In the older specimens the males are always of less weight than the females and the frog of 47 grams was no doubt correspondingly as fully developed as the females weighing 13 and 16 grams more. This practical cessation of progressive changes in the relations of the distal excess at 47 grams is further indicated in some of the succeeding columns of the table.

5. The percentages of the distal excess in the individual nerves (col. H) are higher in the Vth and VIth nerves than in the IXth, as was noted in Table I, and they also show a decided though irregular increase in value with the increase in body weight. When again the percentage of the sums of the distal excess based upon the sums of the fibers in the two roots of each set of nerves is considered (col. I) it is seen that the value increases gradually, and much more regularly, with the increase in weight. From this it is evident that not only does the general distal excess of fibers increase with the growth of the animal, but that it increases at a more rapid rate than the number of fibers in dorsal and ventral roots. This suggests the question as to which of the two roots undergoes growth changes more nearly corresponding to those manifested by the distal excess. In column J the relation of the sums of the distal excess to the sums of the dorsal root fibers in each set of nerves is expressed in the form of percentages and in column K the same is done for the ventral root fibers. As shown in Table I, the number of dorsal root fibers is always greater than the ventral root fibers and so the sum of the distal excess in the smallest specimen is 14.4% of the sum of the dorsal root fibers and 24.4% of the ventral root fibers. The percentages of the ventral root vary in a more regular and constant progression than those of the dorsal root. From this it may be assumed that the changes in the number of the ventral

root fibers more nearly keep pace with the changes in the distal excess. It is shown in Table IV that the ventral root gains fibers somewhat more rapidly than the dorsal root. The percentage variations in the ventral roots of the individual nerves cannot be shown so well in a single column as the sum relations, for, in 6 out of the 14 smaller nerves (the nerves which possess relatively the largest distal excess), the distal excess exceeds the number of fibers in the ventral root.

6. The variations in the distal excess do not closely coincide with the variations in the number of fibers in the trunks and dorsal branches (col's. F, A and B and col's. G and C). Yet when the percentage relations of the sums are considered (col. N) there is again evident a fairly regular and progressive increase. This indicates further that the fibers forming the distal excess increase at a proportionately more rapid rate than the sums of the trunks and dorsal branches in which the excess is contained. The excessive increase is similar to that relating to the two roots though less rapid and somewhat more irregular. In Table IV it is better shown that as the animal grows it gains fibers more rapidly in the trunks and dorsal branches than in the nerve roots. It is indicated here that some of this more rapid gain must take part in forming the distal excess.

7. As pointed out in the previous papers, the value of the distal excess is dependent upon or somehow correlated with the relative amount of the dorsal branches. Those nerves which have a proportionately large number of fibers in their dorsal branches as compared with the number in the nerve trunk always have a high percentage of distal excess. Most of the smaller nerves of the frog are of this type. Of the 14 smaller (Vth and VIth) nerves employed here, 6 have dorsal branches containing even more fibers than the trunks themselves (compare col's. A, B and H). All of them have higher percentages of distal excess than the IXth nerve. While in the individual nerves (col. B) as well as in the sums (col. L) it is seen that dorsal branches increase with the body weight, the variations do not appear so regular or to closely coincide with the variations in the amount of the distal excess (col's. F and G). A

comparison of their numbers alone shows that the dorsal branches contain many fibers which have nothing to do with forming the distal excess for in every case here the dorsal branches themselves contain at least a few more fibers than comprise the distal excess. However, in the nerves formerly dealt with it was found possible in some of the larger nerves, for the distal excess to exceed the amount of the dorsal branches thus making it necessary, in those cases at least, that some of the distal excess be contained in the trunk. The percentage relations of the amount of the distal excess to the amount of the dorsal branches are shown in column M. In this it is seen again that the distal excess increases at a more rapid rate than the number of fibers in the dorsal branches, though the progression is not so constant as in some of the other cases. If the fibers of the dorsal branches alone are concerned to any great extent in forming the distal excess, the relation of their number to the number composing both the trunk and dorsal branches should be somewhat similar to the same relation maintained by the amount of the distal excess. In column O such relations of the dorsal branches are expressed in percentages and when they are compared with the same values for the distal excess (col. N) the variations of the two are not very similar. Rather, a more fixed proportion is manifest, the dorsal branches comprising approximately 19 % of the fibers on the distal side of the ganglion up to 47 grams at which specimen the proportion suddenly changes to 24 %.

8. Certain of the excess of cells in the spinal ganglion above the number of fibers in the dorsal root may take part in contributing to the distal excess. In column P are given the numbers of cells in the spinal ganglia in excess of the fibers in the respective dorsal roots and in the last column of the table the relations of the fibers of the distal excess to these extra cells are expressed in the form of ratios. Though it appears that the cells themselves increase with the increase in weight, the increase of the fibers in the distal excess is such that while in the youngest specimens there are twelve times as many cells as fibers, in the 47 gram frog there are only six times as many.

This shows it possible that some of these extra ganglion cells may send processes toward the periphery alone and thus contribute to the distal excess. It is further seen in the columns that if the cells of the ganglion increase in number, their increase does not keep pace with that of the distal excess, nor does the number of cells in excess of those giving origin to dorsal root fibers bear a constant relation to the fibers forming the distal excess.

As to *the origin of the distal excess*, it is indicated in the number relations noted above that it can hardly be due to any one cause. To explain its existence little can be added in this paper to that which was advanced in the previous papers. There are very few publications which even consider its presence, but certain of the findings of several investigators upon the structure of the spinal ganglia may be interpreted toward its explanation.

One of the first explanations which suggests itself is that the excess may be due to the splitting of fibers on the distal side of the spinal ganglion. This was one of the first evidences sought for by the author. Both methylen blue *intra vitam*, and gold chloride were employed in the preparations and serial sections as well as teasing were resorted to. The Vth and VIth nerves were chiefly used for this because they are the smaller of the nerves used in this paper and because the smaller nerves have the higher percentage of distal excess.

A bifurcation of the fibers on the peripheral side of the ganglion was observed quite often but by no means was it observed in sufficient frequency to at all explain the entire origin of the distal excess. To give a distal excess of even 10%, every tenth root fiber must bifurcate at the peripheral border of the spinal ganglion and, while with the methods employed it was impossible to determine the exact proportion of dividing fibers, the author is convinced that it cannot occur even as frequently as this. It is seen in the tables that the smaller nerves always have a distal excess above 10% and that it may even exceed 50%. Most of the splitting observed occurred within the level of the peripheral border of the ganglion, and in order

to correctly interpret each case, the ends of the fiber had to be followed sufficiently to preclude the possibility of the T-fibers of RANVIER or those of DOGIEL cells being mistaken for the type of bifurcation sought. As the fibers from the two roots join to form the trunk and dorsal branches, they cross and intertwine to an extent which renders teasing or following a fiber in sections quite difficult. Owing to tearing and breaking and the difficulty in following a fiber in question through the maze, certain of the bifurcations observed had to be discarded as uncertain. But including the uncertain cases would not have made enough to account for the average distal excess. The great majority of the fibers on the distal side of the ganglion show no branching at all.

For the same reasons I was especially unable to determine the proportion of the dividing fibers belonging to each root separately. Bifurcations of ventral root fibers are somewhat more easily distinguished than those of fibers arising in the spinal ganglion. Of them it can only be said that they are certainly not frequent enough to give percentage values similar to those in column K, Table III. In most of the cases a ventral root fiber was seen to bifurcate, sending one product of the division to the dorsal branches while the other remained in the nerve trunk. This is of interest physiologically for the muscle supplied by the dorsal branches and by the trunk are usually considered independent. It is not an unheard-of complication however. CAJAL ('99) pictures such an occurrence in the chick and discusses it physiologically, and DUNN ('02) finds frequent divisions of fibers in the sciatic of the frog, one product going to a branch supplying one muscle or set of muscles and the other going on in the trunk to be distributed to other muscles entirely distinct. Most of the fibers going from the ventral root to the dorsal branches do not bifurcate. Occasionally a fiber divides after entering the dorsal branches, its parts going to different divisions of the branches. If such a splitting occurs near enough to the spinal ganglion to be included in the section used in the counting, it of course would contribute to the distal excess.

Some years ago STANNIUS ('49) and FREUD ('78) observed splitting of the peripheral process of the spinal ganglion cell, the former in fishes and the latter in Petromyzon. DOGIEL ('96) describes the same for mammals and BÜHLER ('98) suggests it as an explanation of the distal excess found by him in the frog. It cannot be of very frequent occurrence in the frog. From my own observation I am led to believe that a splitting of the peripheral process of the dorsal root ₍neurone is less frequent than in the ventral root fibers. Of the different frog's nerves examined here only three cases of the bifurcation of this process was observed. In these one product went to the dorsal branches and the other continued in the nerve trunk. DOGIEL (p. 148) pictures this arrangement occurring in mammals. DO- GIEL ('97) also finds division of axones in the dorsal root or on the central side of the spinal ganglion.

It may be further added in explaining the distal excess that if it were mostly due to the splitting of fibers representing the two roots, then for it to obtain the rate of increase mani- fested, these fibers would have to either divide with increasing frequency as age advances or they would have to give off branches (divide) after they have grown into the nerve and become me- dullated. The latter at least is hardly probable, though it might be urged in support of it that the bifurcation always occurs at a node in the sheath. I know of no observations directly sup- porting either idea.

The greater source of the distal excess lies perhaps in the presence of fibers connected with the spinal ganglion but not represented in the nerve roots at all. Such fibers are of sym- pathetic origin and have been repeatedly described (CAJAL, '93, HUBER, '94, DOGIEL, '96a, CAJAL, '99 and others) as entering the spinal ganglion and breaking up into numerous twigs which terminate in telodendria about the cells there, mostly the DOGIEL cells of Type II. Many of these sympathetic fibers are described as medullated. In my preparations of the frog, by comparing sections of the ramus communicans with sections of the trunk and dorsal branches, there may be seen in the lat- ter numerous medullated fibers similar to those considered of

sympathetic character in the ramus. They belong to the smaller type of fibers. The larger of them have a medullary sheath which is relatively thinner than that of fibers of undoubted spinal origin and which stains less black with osmic acid and shows a tendency to collapse in the sections. The smallest of the medullated fibers in the rami, however, cannot be distingushed from the smallest of the fibers known to arise in the spinal cord and spinal ganglia. Otherwise differential counts could be made to determine their exact ˈproportion in the trunk. As is well known, the rami contain fibers from both the ventral roots and spinal ganglia. The larger of these may be distinguished by the character of their sheaths.

Fibers considered of sympathetic character were always observed in the dorsal branches. When the dorsal branches are much divided, often a small twig may be seen with the majority of the fibers in it of this type. This suggested that fibers from the sympathetic ganglia may enter the nerve trunk by way of the ramus, traverse it to the peripheral border of the spinal ganglion and there pass into the dorsal branches without connecting with the spinal ganglion. Such fibers would of course be counted twice, once in the trunk and once in the dorsal branches and thus contribute to the distal excess. A special search was made for such fibers and none were found which could be so construed with certainty. If any exist they must be very few and it was assumed that the distal excess cannot be very materially affected by them. I think it necessary to explain at least most of the sympathetic fibers in the dorsal branches in some other way, and suggest that certain of the so-called multipolar cells in the spinal ganglia have to do with them. There are numerous observations (cited above) noting the presence of these cells and many ascribed to them a sympathetic character—cells left over in the spinal ganglia during the period of the offshoot of the anlage of the sympathetic. Telodendria of the centripetal sympathetic fibers are described as terminating about these cells and the role presumed for them here is that they are merely interposed in a sympathetic chain of neurones and that the fibers given off by them pass by way of the dorsal

branches to the blood vessels, etc., proximal to the vertebral column. Such an arrangement would give two extra fibers on the peripheral side of the spinal ganglion. It should be mentioned, however, that DOGIEL ('97) who has made a study of these cells, was unable to trace any of their processes beyond the confines of the spinal ganglion. He considers them either sympathetic or modifications of his spinal ganglion cell of Type II.

Finally let it be added that early in this investigation counts were begun of the medullated fibers in the rami communicantes with the hope of gaining some clue as to the proportional part they play in forming the distal excess. It was soon found that the number of fibers in the distal excess of a nerve is often greater than the number of medullated fibers in its ramus and since many of the fibers of the ramus are of undoubted spinal origin and many of the smallest of uncertain origin, the research was discarded as unprofitable in that the ramus cannot account for all of the excess and in that it was impossible to determine the exact proportion it does contribute. So far the conclusions must be general, namely, that the distal excess is due to several causes, though probably the greater amount of it is due to medullated sympathetic fibers connected with the spinal ganglion but which are not continued into the nerve roots.

VI. The gain of cells and fibers with the gain of weight.

BIRGE ('82) determined that the frog while increasing from 1.5 grams to 111 grams gained in the ventral roots of its entire spinal nerve 51 fibers for each gram of weight gained. This estimation was based upon counts of all the ventral roots of one side of 6 specimens. He also counted the dorsal root fibers of one side of two frogs, one weighing 23 and the other 63 grams. Computations based upon the numbers he obtained give for all the nerves of both sides a gain of 77 dorsal root fibers per gram of weight gained. His data are not sufficient upon which to base estimations of the gain of fibers on the distal side of the spinal ganglion. The author ('00) dealing with the VIth spinal nerve alone of frogs varying from 5 to 79 grams, ob-

tained numbers indicating a rate of gain in this one pair of nerves of about 3 ventral root fibers, 5 dorsal root fibers, and

TABLE IV.

(Frog)

Body weights in grams.	A Sums of cells in spinal ganglia of the three nerves.	B Sums of fibers in the dorsal roots of the three nerves.	C Sums of fibers in the ventral roots of the three nerves.	D Sums of fibers in the trunks and dorsal branches of the three nerves.	E Sums of fibers in the dorsal branches of the three nerves.	F No. of cells in ganglia per fiber in dorsal roots.	G Ratios of ventral root fibers to dorsal root fibers.
33.7	6189	2316	1416	4205	808	2.7	1:1.6
47.4	5201	1933	1647	4166	1022	2.7	1.2
61.8	7328	2294	1509	4384	1049	3.2	1.5
63.4	6771	2141	1283	4039	974	3.2	1.7
Totals: 206.3	25489	8684	5855	16794	3853	2.9	
Averages: **51.6**	**6372.2**	**2171.0**	**1463.7**	**4198.5**	**963.2**	**2.9**	**1.5**
7.0	5105	1888	1115	3275	620	2.7	1.7
10.4	6244	1723	962	2968	570	3.6	1.8
25.3	4462	1667	943	2903	534	2.7	1.8
Totals: 42.7	15811	5278	3020	9146	1724	3.0	
Averages: **14.2**	**5270.3**	**1759.3**	**1006.6**	**3048.6**	**574.6**	**3.0**	**1.7**
Differences of averages: **37.4**	**1101.9**	**411.7**	**457.1**	**1149.9**	**388.6**		
Gained per gram of wt. gained: **1**	**27.8**	**11.0**	**12.2**	**30.7**	**10.4**		
% of gain:	**20.9%**	**23.3%**	**45.4%**	**37.7%**	**58.9%**		

TABLE IV. The base numbers are taken from Tables II and III. The specimens are entered in two groups, one of the four larger frogs, the other of the three smaller. Opposite the individual body weights are the sums of the ganglion cells and of the nerve fibers in the localities indicated of the three nerves. The table allows a comparison of the number of cells the average specimen of each group would possess in the spinal ganglia of the three nerves (col. A), and of the number of fibers in the dorsal roots (col. B), ventral roots (col. C), the trunks and dorsal branches combined (col. D), the number of fibers in the dorsal branches alone (col. E), and finally the ratios of the ganglion cells to the dorsal root fibers (col. F) and the ratios of the fibers in the ventral roots to the fibers in the dorsal root (col. G). In the last two lines across the table are given (1) the estimated number of cells and of fibers in the given parts of the nerve gained per gram of weight gained and (2) the gains in proportion to the numbers contained in each is expressed in percentages.

10 fibers in the trunk and dorsal branches for each gram gained in weight. This estimation was based on upon counts from 12 specimens.

TABLE V.

(White Rat)

Body weights in grams.	A Sums of cells in spinal ganglia of the three nerves.	B Sums of fibers in the dorsal roots of the three nerves.	C Sums of fibers in the ventral roots of the three nerves.	D No. of cells in ganglia per fiber in dorsal root.	E Ratios of ventral root fibers to dorsal root fibers.
69.0	28897	6420	2567	4.5	1:2.5
167.0	29048	7393	3115	3.9	2.4
Totals: 236.0	57945	13813	5682	4.2	
Averages: **118.0**	**28972.5**	**6906.5**	**2841.0**	**4.2**	**2.4**
10.3	26453	3328	1177	7.9	2.8
24.5	25061	4343	2139	5.8	2.0
Totals: 34.8	51514	7671	3316	6.7	
Averages: **17.4**	**25757.0**	**3835.5**	**1658.0**	**6.7**	**2.3**
Difference of averages: **100.6**	**3215.5**	**3071.0**	**1183.0**		
Gained per gram of wt. gained: **1**	**31.9**	**30.5**	**11.7**		
% of gain	**12.5%**	**80.1%**	**71.4%**		

TABLE V. Compiled from figures given by HATAI ('02) Table VII and ('03) Table III for the VIth cervical, IVth thoracic and IInd lumbar nerves of four white rats of different ages. Constructed in the same way and showing the same relations as Table IV. (Note: In the two papers of HATAI there are some slight discrepancies in the body weights. For example, in one paper the results from a 68.5 gram rat are given in the other paper as obtained from one of 69 grams, and a specimen of 24.5 grams in one paper is given 25.4 in the other. These are considered oversights or misprints and of little importance anyway. The only specimen mentioned in the second paper as additional had a weight of 264.3 grams and it is not included here since its ganglion cells were not counted.)

These indications of the rate of gain of the nerve fibers with growth suggest similar estimations for both the nerve fibers and the ganglion cells of the nerves dealt with in this paper. The results of such estimations and the method by which they are made are shown in Table IV. And in order to compare the conditions

in the nerves of the frog with those in a mammal, the figures obtained by HATAI ('02 and '03) for the white rat are compiled and arranged in the same way in the accompanying Table V. HATAI also used but three nerves.   So far as I know his results are the only available for such a comparison.   In both tables the numbers apply to the nerves of one side of the body only and therefore must be doubled for the approximate numbers for both sides.

In the first place, it is further shown in Table IV that the average younger frog possesses a good many more cells than fibers in proportion to its weight than the older.   It was shown in the previous papers that the younger gain fibers at a more rapid rate than the older.   This is not so evident in the three nerves used here from the fact that the IXth nerves of the younger contain considerably above the usual relative proportion of fibers and thus produce larger sums for the three nerves.   In the rat HATAI finds that the gain in the younger is considerably more rapid than in the older.

It is also shown in Table IV (col's. B, C, D and E) that as the frog increases in weight, for each gram of weight gained, there is an apparent gain of 11 dorsal root fibers, 12.2 ventral root fibers, 30.7 fibers in the trunks and dorsal branches and 10.4 fibers in the dorsal branches alone.   Compared with results obtained in a similar way from BIRGE's figures, such gains in only three of the nerves of one side appear rather high.   However, as was previously seen ('00), *Rana virescens* seems to possess an appreciably greater number of fibers in its spinal nerves in proportion to body weight than does the European *Rana esculenta* employed by BIRGE and therefore to maintain this, its absolute gain of fibers per gram of weight gained must be greater.

It is also evident that apparently the ventral root gains fibers at a somewhat more rapid rate than the dorsal root, the relations being 12.2 to 11 per gram gained.   In the previous paper, in the VIth nerve alone, the advantage seemed to be with the dorsal root, the ventral root gaining but 1.4 fibers to 2.4 gained by the dorsal root.   Computations from the figures available

for the purpose in BIRGE's records give for all of the spinal nerves also a higher gain in the dorsal root. And HATAI's counts ('03) for the rat, when tabulated in a similar way (Table V), show a considerably greater absolute gain of fibers in the dorsal root per gram of weight gained. The dorsal roots of all the spinal nerves here used of the frog and all of those used by HATAI of the rat contain many more fibers than the ventral roots (col. L, Table I and col's. G and E, Tables IV and V). One would therefore expect the absolute gain to be greater in the dorsal root. But the gains in proportion to the number of fibers contained in each may show differently. It is seen in column C that the three ventral roots of the average frog of 14.2 grams gain about 45 % in fibers with the increase to the average weight of 51.6 grams while the dorsal roots (col. B) gained but 23 %. By comparing percentages of gain in this way it will be found that the figures for the VIth nerve alone in the paper above referred to also give a somewhat greater gain in the ventral root. By grouping HATAI's figures in the same way (Table V) the dorsal roots appear to gain 30.5 fibers per gram of weight gained, while the ventral roots gain only 11.7 fibers and, in proportion to the fibers contained in them, the dorsal roots gain 80 % and the ventral roots 71 %—a group result still in favor of the dorsal root. However, HATAI makes it one of his conclusions that the increase of medullated fibers in the ventral root is more rapid than in the dorsal root. He reaches this not by grouping as above, but by simply comparing the relations of the nerve roots of the youngest rat with those of the adult individual. In column E of Table V it is seen that in the 10.3 gram rat, for each fiber in the ventral root there are 2.8 fibers in the dorsal root, while in the 167 gram rat the ratio is 1:2.4, thus showing that, as far as these two individuals are concerned, the increase of ventral root fibers must gain on that of the dorsal root fibers during the growth of the animal. When, on the other hand, the ratios of the groups are considered it is evident that in the younger the average ratio of ventral root to dorsal root fibers is 1:2.3 while in the older it is 1:2.4, thus indicating a slightly more rapid increase in the dorsal roots. The same ratios

in the frog (col. G, Table IV) do not vary as much as they do in the rat. In fact, the extremes, the specimen of 7 grams and that of 63 grams, show similar ratios between their ventral and dorsal root fibers. The group or average ratios, however, indicate the more rapid increase of ventral root fibers mentioned above.

Table IV further corroborates a relation indicated in the foregoing tables. Column D indicates that in the sums of the trunks and dorsal branches combined there is a gain of 30.7 fibers for each gram gained in weight. This is a greater gain than in either root or in both roots combined. In proportion to the number of fibers contained in them, the gain in the trunks and dorsal branches is only 37.7%, or less than the percentage gain in the ventral roots. But the percentage rate is made up in the dorsal branches considered separately (col. E). Here the gain is about 59%. This again suggests that some correlation exists between the dorsal branches and the distal excess, for as shown, the distal excess increases at a more rapid rate than the fibers in either the dorsal root, the ventral, or in the trunk and dorsal branches.

The question of the ganglion cells is rather puzzling. The tenet more usually held is that in the vertebrates the number of nerve cells is fixed at quite an early stage in the development. This belief applied to the frog precludes an increase in the number of spinal ganglion cells even at the youngest stages employed here. Yet, when the numbers of ganglion cells found in the different specimens are considered in the same way as the fibers in the nerves which admittedly increase with growth, the cells appear to undergo, in their sum relations at least, variations somewhat similar to those of the fibers. As arranged in Table IV (col. A) it is indicated that for each gram the frog increases in weight, there is a gain of 27.8 cells in the spinal ganglia, or, as the average specimen increases from 14 2 grams to 51.6 grams, the cells undergo an increase of 20.9%. This percentage increase is less than that of the fibers as must be the case, but it is surprising that it appears so nearly equal to it.

It is seen (col. F) that in the younger specimens the num-

ber of cells per fiber in the dorsal root is greater than in the older specimens, but the difference is not so great as one would be led to expect nor do the ratios of the individual sums show a variation decreasing with the increase in weight. Rather, the relations between the number of cells and the number of dorsal root fibers seem to be maintained approximately constant in the nerves here employed. All this can hardly be due to chance variations in the fixed number of cells in the individual ganglia of the different frogs.

With HATAI's enumerations for a mammal, the results are different. Using a similar tabulation of his numbers for the three nerves of the rat (Table V) it appears that, with the increase from the average weight of 17.4 grams to that of 118 grams, the ganglion cells undergo an increase of only 12% while the dorsal root fibers increase 80% and the ratio between the two is considerably higher in the younger than in the adult. HATAI ('02) notes that in some of the nerves of the rat of 10.3 grams, the ratio of fibers to cells is as much as 1:11, while in the older it may be as low as 1:3. Based on this great decrease of the ratio with the progress of growth and the relatively small actual increase in the cells of the individual nerves of the different specimens, he concludes that the number of ganglion cells in the white rat remains approximately constant between the weight of 10.3 grams and the adult. He interprets the differences as probably due to individual variations in the ganglia of the different specimens employed and cites the fact that the 24.5 gram rat gives a sum of cells in the three nerves chosen which is less than that of the rat of 10.3 grams. DONALDSON ('02) supports the views of HATAI and in discussing the investigation, lends observations which strengthen it.

HATAI states that the only argument in favor of an increase in the number of cells with age is the fact that of the four specimens employed the two older gave combined a greater number of cells than the two younger. Table V here given groups the older against the younger in order to compare the results with those from the frog in Table IV. The difference between the averages of the two groups of rats amounts to about 3200 cells.

In the frog at least, that in a limited number of nerves an older animal may show fewer cells than one somewhat younger, can be equally well explained as due to the fact that the proportional number of neurones apportioned to a given spinal nerve is by no means constant.

The progress of growth in the frog is evidently different from that in the mammal. The 7 gram frog is no doubt relatively more developed than the 10 gram rat and in the rat of 10 grams and younger the processes of growth must go on much more rapidly. This I think is indicated in the two tables.

While the number of ganglion cells may not increase with age in the rat, the evidence though slight is, I think, a little stronger for the frog. It is needless, perhaps, to go into the literature for the support of this view for so far as I am aware, there are no observations which directly maintain it. Bühler ('98) in discussing the cells of the spinal ganglia suggests that the large cells are continually degenerating while the small cells enlarge and replace them. If this were true, the cells would have to multiply or else the number would, on the contrary, decrease with age. Of the 18 papers that I know of, which, dealing with tissues more or less mature, describe appearances in nerve cells (vertebrate and invertebrate) thought to be concerned in the processes of cell division, none of them describe cases of undoubted nerve cells which can be confidently considered the actual process of division. Of the list Lenhossék ('95), Dehler ('95) and Bühler ('98) describe such appearances in the spinal ganglion cells of the frog.

Summary.

1. Due to variations in the relative number of neurones apportioned to a given spinal nerve, the number in a given nerve may not increase regularly with the increase in body weight but the sum obtained by adding the numbers in a given nerve of the larger specimens, as well as the sum of the several nerves of the larger specimens, is always greater than that of the smaller specimens.

2. In the average there are nearly twice as many nerve fibers in the dorsal root as there are in the ventral root of the Vth, VIth and IXth nerves. The average is the highest for the Vth and in both the Vth and VIth is higher than in the IXth nerve. This agrees with the nature of the innervation supplied by the smaller nerves.

3. As compared with the corresponding trunk, the number of nerve fibers contained in the dorsal branches is relatively much greater in the Vth and VIth than in the IXth nerve, while in actual amount, the average number of fibers in the dorsal branches of each of the three nerves is similar.

4. The distal excess, or the excess in the sum of the fibers of the nerve trunk and dorsal branches above the sum of the dorsal and ventral roots, occurs to an appreciable extent in every case. While it is less in the nerves of the smaller specimens, its average amount in each of the three nerves of the several specimens is similar.

5. The percentage of the distal excess ranges higher in the Vth nerve than in the VIth and it is much higher in both than in the IXth nerve.

6. There is a general average of three times as many cells in the spinal ganglia as there are fibers in the dorsal roots. And there are more than twice as many ganglion cells as there are fibers in the trunk and dorsal branches less the number of fibers in the ventral root. The average ratios for each of the three nerves are similar, being somewhat higher in the Vth and VIth than in the IXth nerves. On neither side of the spinal ganglion do the ratios of cells to fibers show a regular or marked decrease with the increase in body weight.

7. The distal excess in the three nerves of each specimen increases decidedly and with considerable regularity with the increase in body weight. · The distal excess increases at a more rapid rate than the fibers in both or in either of the nerve roots, and also at a more rapid rate than the fibers in the trunks and dorsal branches combined or in either separately. With increasing weight, the variations in the ventral roots coin-

cide more nearly with the variations in the distal excess than do the variations in the dorsal roots.

8. With the increase in weight, the fibers on the distal side of the spinal ganglion increase in number more rapidly than do the sums of the dorsal and ventral roots. In proportion to the fibers contained in them, the dorsal branches gain fibers at a more rapid rate than any other part of the nerve. This more rapid increase of the distal fibers is in some measure an expression of the more rapid rate of increase of the distal excess.

9. Supported by direct observations, the distal excess is explained as due to three causes: (a) Centripetal medullated fibers from the sympathetic system which enter the spinal ganglion to branch and terminate about the cells there; (b) The bifurcation of ventral root fibers on the distal side of the spinal ganglion; (c) The bifurcation of the peripheral axone of the spinal ganglion neurone. In most of the bifurcations observed, one product of the division joins the dorsal branches while the other remains in the nerve trunk. The observed divisions of the fibers of the dorsal branches themselves may take part in producing the distal excess. There are some indications supporting the assumption that certain of the excess of cells in the spinal ganglion may also contribute to the distal excess by sending processes into the periphery but not toward the central system.

10. With the increase in body weight the ventral roots of the Vth, VIth and IXth nerves gain fibers at a more rapid rate than do the dorsal roots, and at a more rapid rate than the nerve trunks considered separately.

11. With the increase in body weight there is an apparent gain in the number of spinal ganglion cells in the three nerves. Between the average weight of 14.2 grams and that of 51.6 grams the ganglion cells increase about 21%, or gain at the rate of 27.8 cells per gram of weight.

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EDITORIAL.

In an earlier number of this *Journal* the need has been urged of some category common to the neurologist and psychologist in terms of which the problems of neural structure and mental function may be discussed without immediately arousing metaphysical prejudices. Such a category is action or behavior. The former is perhaps the more abstract concept and hence will lend itself more readily to the discussion of the philosophical questions which sooner or later are bound to arise. The latter has the advantage of being a term of popular as well as of scientific usage and is more commonly employed to describe the action of organisms. Mr. MORGAN's latest book is entitled "Animal Behavior" and under this term he is successful, for the most part, in discussing the actions of organisms without prejudging the nature of the question of the psychical and its relation to the material processes. Likewise Mr. JENNINGS in the valuable article which appeared in the last issue of the *Journal* discusses the behavior of Paramecium in terms of "action-systems" in a way which does not preempt the field for either the mechanical or teleological interpretation of the phenomena. Researches carried on in this spirit are greatly needed at the present time. Only thus is it possible to construct a platform whose planks shall consist of facts interpreted in terms of a common technique.

It is too early in the history of the movement to predict in detail the lines along which the two sciences will get together, but it is safe to say that there will have to be considerable revision of working concepts on the part of both neurology and psychology. By this is meant that the newer insight into the energic nature of matter will in time inevitably

affect the biologist's conception of the nature of what he calls an organism. Biology, in so far as it pretends to be an exact science, regards the organism as a complicated mechanism whose elements are to be understood in terms of the physical laws which hold for these elements outside the organism. Hence, if, for example, the study of the electrical properties of matter results in transforming our chemical and physical notions, and some form of an energic is substituted for the atomic theory, this dynamic view ultimately must reach into biology with transforming effect.

In a similar way, the conception of the nature of consciousness is undergoing reconstruction in psychological science, in part due to this same energistic theory which is transforming physical science. The traditional formula which is satisfied to postulate a soul back of consciousness, just as it postulates material atoms back of motion or force, appears likely to be eclipsed by the results of inquiries which seek to discover the nature of the intimate relation which certainly seems to exist between mind and matter. There is no blinking the facts of brain structure nor of mental functioning; the problem is to understand what we mean by each in terms of the other.

This it has been almost impossible to do in the past because of the diverse historical conditions and techniques associated with the two sciences. Biology had its roots in the natural and positive sciences; psychology arose as a branch of philosophy and was long known as "mental philosophy." But now that the basis has been laid for a scientific psychology, there is hope of its being possible for the psychologist and neurologist to get together in their work on this common problem.

As has been intimated, this will involve a revision of psychological conceptions on many fundamental points. That this is already taking place is evident from recent tendencies in psychological thought. Consciousness is coming to be stated more and more in terms of action, in terms of the motor aspect of the organic circuit, instead of being stated exclusively in terms of the sensory aspect, which was the tendency with the older intellectualistic psychology. Great emphasis is now being placed

on the motor character of attention, on the dynamogenic nature of ideas, on ideomotor impulses, on tactile-kinaesthetic imagery, on the emotions as vestiges of motor attitudes, on the growth of voluntary movement, on the constructive and reconstructive character of thought. Says Mr. MARSHALL: "We are compelled to assume a unity of process in conscious life. From this point of view, the distinctions between reflex and instinctive activities and between habit and instinct are not fundamental. The sharp distinction between instinct and intelligence implies denial of the unity of consciousness" (*Mind*, Vol. XI, No. 44). Professor LLOYD says: "Nothing in philosophy is so much needed at the present time as the adjustment of the science of abstract thought to the science of organic action, and every little hint as to how this adjustment can be brought about cannot but be at least a little help. The evolution of consciousness must be almost meaningless until the simplest case of accommodation as seen by the biologist is identified with the most perfect case of abstract thought that the logician knows" (*Psy. Rev.*, Vol. III, p. 426). And a recent writer has gone so far as to define perception as "an attitude toward the object perceived." He says: "Perception is an attitude toward an object as well as a complex of sensations." "All that objects mean to us is largely due to the sensations that flow backward from the bodily reverberations they excite directly in us. Perception is an attitude toward the objects perceived" (BOLTON, Biological View of Perception, *Psy. Rev.*, Vol. IX, No. 6).

How far these particular suggestions may prove fruitful in bringing about the desired synthesis is a matter of relatively little moment here. The important consideration is to note the fact of this tendency in recent literature and to keep in touch with the almost kaleidoscopic changes which are marking the progress of the comparative method as employed in this field.

The further investigations of animal reactions are carried, the more difficult appears the problem of the distribution of consciousness. But, as if to counterbalance this, the further research in comparative psychology is carried, the more is the conviction forced upon the investigator that the reactions of

human beings (including their psychical processes, their conscious acts) will never adequately be understood until we have formulated the laws of the behavior of these simpler types of organisms.

The value of a study of the animal mind for human psychology has been emphasized by various writers. But its full significance, methodologically, has not always been realized. This deeper significance lies in the dynamic conception of consciousness, as itself a phase of the ultimate energic system, a balance or tension of forces, admitting, like all other energic phenomena, of examination, description and explanation. The conditions of consciousness as represented in the complicated structures of the brain in the higher forms are too intricate to admit of exact statement as yet in scientific terms. Hence the promising character of researches upon the lower forms where the conditions are simpler, and where, if anywhere, the precise function of the brain as an organ for the transformation of energy can be determined. Here first may we expect the laws of equilibration or tension of energies which we call conscious to be elucidated. The solution of the deepest problems of psychology, there is good reason to believe, lies in the hands of the comparative psychologist.

SCHULTZ, in a recent article entitled "Gehirn und Seele" (*Zeitschr. f. Psy. u. Physiol. d. Sinnesorg.*, XXXII, Heft 3 u. 4, pp. 246-7) calls attention to the apparent dilemma in which the comparative psychologist finds himself. It is certainly a safe assumption that the higher, more complicated mental life of man and the higher animals can best be explained by a knowledge of the simpler conditions of mental life in the lower forms. On the other hand, it is a general principle that in explanation we should proceed from the known to the unknown. Now my own human individual consciousness is best known to me and most immediately given. We here seem to be under the compulsion equally of following what Professor BALDWIN has called the "leveling up" and the "leveling down" methods, the mechanical and the teleological (or what some would call the anthropomorphizing) tendencies.

The limitations of the one method lie in the incredible chasm in degree (if not in kind) which must lie between my complicated conscious life and that of the simplest organisms (if they have any at all). This would seem to check any anthropomorphizing tendency at the start. BINET's mistake, for example, lies not chiefly in his assumption that the lower organisms have consciousness (this may or may not be true), but in his uncritical use of the categories of adult human psychology in describing the reactions of micro-organisms. It is, of course, an inference that any organism besides my own has consciousness, but it is an inference, in certain cases, of extreme probability. But that perception, association, preference, choice, mean the same in these lower forms is a point to be demonstrated, not to be assumed. The great need of comparative psychology at the present time is the reduction of human conscious reactions to the lowest terms, especially as they are represented in the human infant, in the savage. and in primitive man, in order to make the comparison between human and animal behavior more direct.

On the other side, the difficulty lies in the fact that the terminology of tropisms and animal reactions has grown up almost exclusively under the domination non-psychological science, with the result that the answer to the question as to the presence of mental life in these lower forms is prejudged from the outstart. Evidently there is need of some common basis of method in biology and psychology. This is supplied, in a general way, in the conception of conscious states as themselves acts, as truly as the more obvious activities of the motor organs, but more subtle because remotely conditioned in the brain processes. One of the common problems thus, of comparative neurology and comparative psychology becomes, as has been said before, the problem of the evolution of action, and particularly the problem of the determination of the conditions of conscious action.   H. HEATH BAWDEN.

THE INTERNATIONAL COMMISSION ON BRAIN RESEARCH.

The idea of appointing a special commission to advise the International Association of Academies as to the means best calculated to advance and coördinate research work on the brain originated, so far as I am aware, with the late Professor His. He formulated a somewhat ambitious scheme, the main idea of which was the foundation in each country of a central institute to, in a sense, control the research work being done in that particular country and to serve as a means of communication with similar institutes in other countries. The function of these institutes was to receive material for research, sent by people who did not particularly want it, and to distribute it to workers to whom it would prove of special value; to receive and store specimens, photographs and other records of research, so that any worker might have the opportunity of examining the actual material upon which published memoirs were based. The author of the scheme hoped that by means of such institutes more uniformity might be introduced in the methods of research, and in the presentment of results; that the data upon which investigations were founded might be rendered more accessible than heretofore and so a common source of disagreement among workers might be removed; and especially that valuable material might be directed into those channels where the best use might be made of it.

To discuss this proposed scheme a special commission of thirty-five members representing fourteen nationalities was appointed. It was subdivided into seven sub-sections of five members each to consider the scheme from the standpoints of (1) Human Anatomy and Anthropology, (2) Comparative Anatomy, (3) Histology, (4) Embryology, (5) Physiology, (6) Pathology and (7) Clinical Medicine.

The Commission met in London in the last week of May without its leader and prime mover, without the one man whose quiet persistency could have brought any measure of success in the realization of his scheme: Professor His died in Leipzig three weeks before the meeting.

Under these depressing circumstances only about twenty of the remaining thirty-four members of the Commission were able to attend the meeting, over which Professor WALDEYER presided. The subdivision into special subsections was abandoned and a general discussion took plaee as to the feasibility of establishing such institutes as the late Professor HIS had suggested. In the public discussion the chief difficulty brought forward against the realization of the scheme was financial— the need for funds to establish and maintain the institutes ; but in private conversation with the members there seemed to be a general concensus of opinion that the scheme was too utopian ; that it was hardly likely that any considerable body of men would be so self-denying as to present their material to an institute for distribution and that the possibility of accomplishing the other objects aimed at in the general scheme seemed to be very slight. However, the members present agreed to strive to make the existing institutions in which each of them was working serve as far as possible the function of such a central institute as had been outlined in the general scheme. This platonic resolution was the only result of the general meeting of the Commission.

At the general meeting Professor EDINGER remarked that this exceptional meeting of neurologists afforded an excellent opportunity to discuss certain problems of general interest, and he proposed that a special meeting be held to discuss the primary subdivision of the vertebrate cerebral hemisphere. At the special meeting, which was presided over by Professor J. N. LANGLEY, Professor EDINGER explained that his chief reason for calling the meeting was to discuss the possibility of devising some primary subdivision of the lowlier vertebrate types of cerebral hemisphere such as I had proposed for the Mammalia. I was requested to explain to the meeting the nature of my subdivision of the mammalian hemisphere and especially the significance of the neopallium. In the discussion, which was carried on chiefly by the chairman, Professors RETZIUS, EDINGER and the writer, it was agreed that it was not possible at present to suggest any satisfactory mode of subdivision which

could be applied to all vertebrates, because the differentiation of structure in the higher groups rendered useless the subdivision which would apply to the lowlier groups.   It was therefore decided to submit the question to further investigation and Professor EDINGER invited me to prepare a report proposing a subdivision, which might be submitted to all those interested in the problem, whether members of the Commission or not, for criticism and suggestions.

The other question brought forward for discussion was the possibility of describing cerebral sulci from their relationship to areas of known physiological significance.   I explained the definite relationship which the calcarine sulcus, the sulcus lunatus (''Affenspalte'') and the superior and inferior occipital sulci present to the visual cortex.   The essential part of the suprasylvian sulcus is a superior limiting furrow of the auditory cortex.   The central sulcus in the Primates is a *posterior* limiting sulcus of the excitable or motor area, whereas the crucial sulcus of the Carnivora is an *anterior* sulcus of the motor cortex.   In time it will probably be possible to describe all the important furrows of the hemisphere in terms of their relationship to certain definite cortical areas and so to correlate the data of morphology and physiology.   The excellent researches of Dr. A. W. CAMPBELL of Liverpool and the well-known work of Professor FLECHSIG are rapidly preparing the way for such an advance.

In the discussion of this matter, in which Professors HENSCHEN, RETZIUS, VON MONAKOW, EDINGER and LANGLEY took part, it was agreed that it was too early to adopt the proposed method of describing sulci.

At other informal meetings various members of the Commission gave demonstrations.   Professor RAMÓN Y CAJAL showed extraordinary specimens of neurofibrillae in ganglion cells stained by his new method and Professor HENSCHEN showed many sections of the calcarine region exhibiting various forms of degeneration in the visual area.

The Commission is to meet again three years hence.

G. ELLIOT SMITH.

LITERARY NOTICES.

Goldstein, Kurt. Kritische und experimentelle Beiträge zur Frage nach dem Einfluss des Nervensystems auf die embryonale Entwicklung und die Regeneration. Three plates and two text-figures. *Arch. f. Entwkmech.*, 1904, **18,** 57-110.

SCHAPER'S experiment which showed motility in a frog larva in which he had destroyed the brain and found the spinal cord in a state of disorganization, left a certain desire for more evidence. WOLFF failed to obtain the same decisive result, and MOSKOWSKI actually considered the claim refuted. GOLDSTEIN, a pupil of SCHAPER, now supplements the first description by a drawing which is more convincing than SCHAPER'S original one, and he adds new experimental material, which shows WOLFF'S error and firmly establishes very important data in harmony with SCHAPER'S observations.

WOLFF divided frog larvae of less than 5 mm. so that the dorsal part contained the entire neural tube, and failed to corroborate SCHAPER. GOLDSTEIN succeeded in keeping both parts alive for five days, through the use of LOCKE'S solution, and he showed that they recover motility in two days. Hence, spontaneous and reflex motility in an early embryonic period does not depend on the existence of nerve conduction of a central organ. Moreover, the ventral piece showed further development; notwithstanding the elimination of the neural tube it reached the size corresponding to a larva of about 6.5 to 7.0 mm. Against these facts any arguments based on laws of regenerative processes have absolutely no weight, since we deal here merely with a primary condition of development.

GOLDSTEIN next turns against certain views of NEUMANN. The latter had concluded that at least for a start in the development of muscles, nervous centers were necessary; that, once started, they would develop independently from the central organ, and, in post-embryonic life the trophic center of cord and brain would again put them into a dependent position. The first point is contradicted by various facts. BARDEEN found that muscle differentiation began before the nerves grew forth from the tube. Also HARRISON demonstrated an inde-

pendent development of muscle with fibrils, striation and sarcolemma after excision of the spinal cord and ganglia in larvae of 2.9 and 3.7 mm. NUSSBAUM, too, admits an independent development of embryonic muscles up to a certain degree—all agree with GOLDSTEIN's result that NEUMANN's first claim is incorrect. His second claim, made in order to explain the persistence of muscles in the amyelic monsters, would not be conclusive on his own assumptions. The muscles need not have degenerated within the short time between the lesion (3d or 4th month) and birth (usually in the 6th or 7th month). In WEBER-ALESSANDRINI monsters the lesion must have occurred at 2-3 months and the animal reached full term ; the muscles were, therefore, degenerated and mere fat layers and tendons. LEONOWA also found the muscles of her case of amyelia extraordinarily fatty. (It seems, moreover, that the condition of the motor nerves in these monsters is not satisfactorially ascertained, but should be of great importance in view of BETHE's claims). HERBST's attempt to attribute a trophic control over muscles to the spinal ganglia is refuted. Taking all the facts together, GOLDSTEIN comes to the conclusion that the central nervous system during a certain early period of development has no demonstrable morphogenetic influence on the developing organism.

The second part of GOLDSTEIN's article furnishes evidence showing that this same rule holds for regeneration. Regeneration need not follow the rules of development. It also depends largely on the age of the animal or embryo. The results in invertebrates are contradictory ; those on vertebrates (BARFURTH), probably favorable to the theory of independence from the central nervous system. In adult Tritons WOLFF thought he had proved the necessity of a nervous influence. He obtained regeneration of a leg after removal of the cord, but with intactness of the ganglia ; when the operation was done while regeneration had begun it was arrested *in all but six cases*. In an experiment of SCHAPER on a Triton larva of 30 mm., an extremity was regenerated after destruction of the cord, and although there was complete absence of sensibility and motility. What nerves there were, came "largely" from the spinal ganglia ; the muscles were normal ; even a piece of 1 mm. of spinal cord had reformed at the posterior end of the cut of the cord.

The conclusion is : In the stage of organ formation (ROUX) the normal development and regeneration take place quite independent of the nervous central system. In the stage of functional development there is, however, a decided influence from the central organ.

A. M.

Davenport, C. B. Statistical Methods with special reference to biological variation. *New York. John Wiley and Sons*, viii + 223, second, revised edition, 1904.

In this edition DAVENPORT has revised and enlarged his hand-book of statistical methods in a manner which greatly increases its value to the student of biological variation. An important new chapter deals with the results of statistical work, several new methods are described, and the bibliography is much enlarged.

The present scope and nature of the book is well indicated by the titles of the several chapters : I. On methods of measuring organisms, II. On the seriation and plotting of data and the frequency polygon, III. The classes of frequency polygons, IV. Correlated variability, V. Some results of statistical biological study.

The work of the publisher is no less admirable than that of the author of this guide to statistical methods. Every student of exact science will find the book serviceable, and no student or investigator of biological variation can afford to be without it. Dr. DAVENPORT deserves much credit for the impetus which his energy and enthusiasm have imparted to biometric research in America. R. M. Y.

Deaver, John B. Surgical Anatomy of the Head and Neck. *Philadelphia*, *P. Blakiston's Son & Co.*, 1904, pp. 770.

This book is printed from the same plates as the author's three volume work on Surgical Anatomy, those sections being assembled which will be of greatest interest to specialists in diseases of the eye, ear, nose, mouth, throat and nervous system. The book will prove useful to these and also to physiologists, psychologists and general readers who require a manual for ready and rapid consultation. The text is brief and clear and the illustrations are admirable. There are 177 full page plates drawn from original dissections, which by themselves constitute a useful atlas of topographical anatomy. All parts are designated on the plates in full, thus permitting the reader to glean much of his information by simple inspection without consultation of the text. The external and gross features of the brain are fully and clearly figured, without, however, any attention to histological detail. The printing and binding are exceptionally good.

C. J. H.

Mendel, E. and Jacobsohn, L. Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie und Psychiatrie. VII Jahrgang. Bericht über das Jahr 1903. *Berlin, S. Karger,* 1904. Price, M. 35.

The Jahresbericht is issued this year in two volumes and, like its predecessors, is indispensable to all who wish to keep abreast of the voluminous literature of neurology and psychiatry. The bibliographies are

grouped by topics and accompanied by critical annotations on the contents of nearly all of the papers cited. Compendious indexes make the whole mass of material instantly available.   C. J. H.

Sfameni, Pasquale. Sulle terminazioni nervose nei genitali femminili esterni e sul loro significato morfologico e funzionale. *Archivio di Fisiologia,* 1904, **1,** 345-384.

In this careful and thorough investigation the author has confined his attention to the nerve terminations in the clitoris and the vulva. Topographically these are of three classes: (a) Intrapapillar nerve terminations; (b) nerve terminations in the reticular layer of the derma; (c) terminations in the subdermal connective tissue. The first and second of these are by far the most important. All of these terminations reduce to the single type of "a nervous organ, with or without an envelop of connective tissue, composed of one or more nerve fibers which, after divesting themselves of their myelin sheaths, if they have any, ramify in and around a granular, nucleated substance."

The nerve corpuscles are not the terminations of the sensory nerves but are peripheral ganglia, corresponding to spinal ganglia, and their function is to bring about a more subtle division and modification of the stimuli. The real terminations are always differentiated ectoderm cells scattered through the epithelium and the superficial layers of the derma, and connected with sensory nerve fibers. There is a bibliography of 46 citations.   J. C. BELL.

Harrison, Ross Granville. An Experimental Study of the Relation of the Nervous System to the Developing Musculature in the Embryo of the Frog. *The American Journal of Anatomy,* 1904, **3,** 197-220.

Observations upon embryos the spinal cord of which had been completely isolated before the appearance of either nerve fibers or contractile substance in the musculature, and upon larvae which were reared in a state of constant narcosis by means of a dilute solution of acetone chloroform. Conclusion: "all of the constructive processes involved in the production of the specific structure and arrangement of the muscle fibers take place independently of stimuli from the nervous system and of the functional activity of the muscles themselves.   G. E. C.

Hardesty, Irving. On The Development and Nature of the Neuroglia. *The American Journal of Anatomy,* 1904, **3,** 229-268.

A study of pig embryos to demonstrate the syncytial nature of the neuroglia as proposed in the author's earlier paper on the spinal cord of the elephant. Attention is called to cells resembling the nerve-corpuscles of the peripheral nerve which encircle the medullating axones of the cord.   G. E. C.

Streeter, George L. The Structure of the Spinal Cord of the Ostrich. *The American Journal of Anatomy*, 1904, **3**, 1-27.

A description of the meninges and the macroscopic and microscopic features of the cord; including noteworthy contributions on the arachnoidea, the relation of the peripheral glia sheath to the sinus rhomboideus, REISSNER'S fiber, and the nuclei marginales. Tabulated measurements and a diagram of the cross-section area, in each segment of the cord, of the funiculi ventro-laterales, substantia grisea, and funiculi dorsales.   G. E. C.

Fürbringer, Max. Morphologische Streitfragen. 1. Nervus trochlearis. 2. Rabl's Methode und Behandlung der Extremitätenfrage. *Morph. Jahrb.*, 1902, **30**, 85-274.

Part I (pp. 86-143) is an important contribution to the morphology of the fourth nerve. It is, in the main, a reply to the criticisms made by RABL and DOHRN upon the author's theory to account for the dorsal origin and the crossing of the nerve in question : viz. that the superior oblique muscles were originally muscles of the parietal eye, and that with the disappearance of that organ the originally right oblique muscle became associated with the left eye, and *vice versa*. A bibliography of 296 titles.   G. E. C.

Van Gehuchten, A. Considérations sur la structure interne des cellules nerveuses et sur les connexions anatomiques des neurones. *Le Névraxe*, 1904, **6**, 83-116.

The author places great emphasis upon the fact that the anatomical independence of neurones, as they are demonstrated by the methods of GOLGI and EHRLICH, is the substance of the neurone theory. He considers that, so interpreted, the neurone theory is not contradicted by a single anatomical fact. Intracellular continuity by means of nets and "nervöse Grau" as proposed by BETHE, NISSL and others is purely hypothetical. Even the auto-regeneration of the axone as demonstrated by BETHE, and VAN GEHUCHTEN repeats this experiment successfully, affects only our idea of the origin of the neurone and does not bear upon the neurone theory proper. While in some nerve cells the fibrillae seem to be independent, in many they clearly anastomose in the dendrite and especially in the perikaryon. This condition refutes BETHE'S and NISSL'S opposition to the idea of polarity of the nerve cell, and supports the neurone theory.

                           G. E. C.

Van Gehuchten, A. Connexions centrales du noyau de Deiters et des masses grises voisines (Faisceau vestibulo-spinal, Faisceau longitudinal postérieur, Stries médullaires). *Le Névraxe*, 1904, **5**, 19-74.

A critical review of recent literature on the subject, and a report

on several of the author's degenerative experiments on rabbits. The Marchi method was supplemented with the methods of indirect Wallerian degeneration and of NISSL. The vestibulo-spinal tract arises exclusively after DEITER'S nucleus and descends in the anterior column as far as the lumbo-sacral region. The spinal portion of the posterior longitudinal fasciculus is exclusively descending. Ascending fibers are found in this tract only within the bulb and mesencephalon. Both ascending and descending heterolateral fibers probably come as inferior arcuate fibers either from the terminal vestibular nucleus or from the tuberculum acusticum. The ascending homolateral fibers arise higher up, probably from the nucleus of BECHTEREW. The striae medullares arise exclusively in the tuberculum acusticum. G. E. C.

Soukhanoff. Contribution à l'étude du réseau endocellulaire dans les éléments nerveux des ganglions spinaux. *Le Névraxe*, 1904, **6**, 75-80.

The endocellular net as observed by the KOPSCH osmic acid method is identical with the GOLGI endocellular net, and is not the same structure as the canaliculi of HOLMGREN and others. G. E. C.

Agababow, A. Ueber die Nerven der Sclera. *Archiv f. mik. Anat.*, Bd. 63, H. 4, pp. 701-709, 1904.

Hyde, Ida H. Localization of the Respiratory Center in the Skate. *Amer. Jour. Physiol.*, 1904, **10**, 236-258.

By the employment of careful and precise methods of experimentation on living skates, Miss HYDE has demonstrated the segmental arrangement of the respiratory center. The animal under observation was placed on a board, and sea-water was passed in a continuous stream through a tube into the mouth. Artificial respiration could in this way be maintained for days. In a skate thus situated the medulla may be separated from the spinal cord and from those portions of the brain lying anterior to it without destroying its function as a respiratory center.

Medisection of the medulla is followed, after the inhibitory effects of shock have passed off, by a resumption of coördinated respiratory movements on both sides of the body. The gill arches of one side may move in a rhythm quite different from that of the opposite side. The spiracles may keep time with the gill arches of their respective sides, or both spiracles may be in rhythm with the arches of one side. From the results of median section of the medulla it became evident that "the centers for the nervous respiratory mechanism in the skate were bilateral, each half controlling the movements of its respective side."

Evidence of the segmental character of these bilateral respiratory

centers was obtained by following medisection with hemisection. One lateral half of the medulla was separated into anterior and posterior divisions by a transverse cut. The arches and spiracle of the uninjured side continued their normal movements. The spiracle and first gill arch, controlled by the anterior division of the opposite side, sometimes exhibited a rhythm which differed both from the rhythm of the uninjured side and also from that of the remaining gill arches of the same side, which were under the control of the posterior division of the lateral half of the medulla. At times the respiratory mechanisms connected with all three divisions of the medulla moved in unison.

Lesions of the different lobes of the medulla indicated that the ganglion cells of sensory respiratory neurones, those of the seventh, ninth and tenth cranial nerves, are situated in the lobus vagi. Motor ganglion cells and neuraxones were found ventrad of the lobus vagi and in the fasciculus longitudinalis posterior.   F. W. C.

Gardella, Eloisa. Azione dell' acido fenico sulla sensibilità gustativa. *Archivio di Fisiologia*, 1904, **1**, 398-402.

From its general anaesthetic properties we would expect phenic acid to cause a rise in the threshold of sensibility to taste stimuli. On the contrary, increasing strengths of phenic acid solution up to 3%, applied for 10 seconds, cause a lowering of the threshold for all four of the tastes, bitter, sweet, salt and acid, most of all for bitter. With a constant 2.5% solution and with varying time the threshold falls rapidly during the first 10 seconds, then rises to the normal at 30 seconds, and from there continues to ascend more slowly to 45 seconds.

                                                            J. C. BELL.

Langley, J. N. On the Effects of Union of the Central Part of the Cervical Sympathetic with the Peripheral Part of the Chorda tympani. *Archivio di Fisiologia*, 1904, **1**, 505-511.

Three cats were operated upon and in 89, 96 and 176 days respectively they were killed and the nerves examined. Experiments upon the operated cats and examination of the nerves led to the conclusion that "the sympathetic fibers had united with the nerve cells on the course of the chorda tympani, and in consequence that sympathetic preganglionic fibers are capable of uniting with other similar cells . . . which occur on the course of the cranial nerves." The observations also showed that "the formation of medullated fibers in a peripheral nerve may be caused by fibers reaching it which are themselves non-medullated."   J. C. BELL.

Carlson, A. J. The Rhythm Produced in the Resting Heart of Molluscs by the Stimulation of the Cardio-Accelerator Nerves. *Amer. Jour. of Physiol.*, 1904, **12,** 55-66.

The author has proved that the cardio-accelerator nerves of molluscs when stimulated electrically produce rhythmical contractions of the resting heart. He is inclined to believe, also, that under favorable conditions the resting mammalian heart may likewise be caused to contract by stimulation of the accelerator nerves. The physiology of the cardiac nerves of invertebrates is of special interest because in some forms accelerator nerves alone are present, in others inhibitory nerves alone, and in others nerves which are both inhibitory and acceleratory.

R. M. Y.

Carlson, A. J. The Nervous Origin of the Heart-beat in Limulus, and the Nervous Nature of Co-ordination or Conduction in the Heart. *Amer. Jour. of Physiol.*, 1904, **12,** 67-74.

"It can now be stated as a fact that in Limulus the origin of the heart-beat is nervous, not muscular, and that conduction of the impulse or the co-ordination of the different parts of the heart takes place through the nerves, not through the muscular tissue." This important conclusion Dr. CARLSON draws from the results of a series of ideally definite and well chosen experiments. He has shown (1) that lesion of the median and the two lateral nerves which supply the heart destroys co-ordination, (2) that cross-section of the heart does not interfere with co-ordinated rhythm so long as the nerves are intact, (3) that heart-beat ceases when the median nerve is severed. The author has found material which is particularly favorable for the study of heart action in its relation to the nervous system, and the importance of his work will be recognized at once by all who have interest in physiology.

R. M. Y.

Schiller, V. Ueber die physiologischen Wirkungen des Delphinins (Hegl). *Arch. f. (Anat. u.) Physiol.*, 1904, 248-255, Taf. VI.

Delphinin paralyzes the vagus endings in the heart to a marked degree.   R. P.

loteyko, J. Mécanisme physiologique de la réaction de dégénérescence des muscles. *Travaux du Laboratoire de Physiologie, Instituts Solvay*, 1904, **6,** 59-78.

The reaction of the muscle which has undergone degeneration because of separation from its nerve argues for contractility of the sarcoplasm, and a qualitative difference in irritability of the sarcoplasm as compared with the fibrillae. The author questions whether there may not be a similar qualitative differentiation of irritability in the substance of the nerve.   G. E. C.

Klein, Fr. Das Wesen des Reizes. Ein Beitrag zur Physiologie der Sinnesorgane, inbesondere des Auges. *Arch. f. (Anat. u.) Physiol.*, 1904, 305-342.

A fundamental attribute of protoplasm is that it is stimulated only by *changes* in the normal or usual external condition. The same thing applies to the nerve endings of the retina, hence certain conditions are possible under which we are blind ("rest blindness"). Two such conditions inducing "rest blindness" have been investigated. These are (a) hindering as much as possible every eye movement, (b) illuminating the eye from an equally lighted ("reizlose") surface. The author thinks it probable that only an increase in the intensity of light can act as a stimulus, never decrease. R. P.

Rothmann, M. Ueber die Leitungsbahnen des Berührungsreflexes unter Berücksichtigung der Hautreflexe des Menschen. *Arch. f. (Anat. u.) Physiol.*, 1904, 256-270.

In dogs and cats the conduction in either ascending or descending direction of the impulses in MUNK's "contact" reflexes of the extremities, is not confined to a single sensory or motor fiber tract. The ascending impulses of the reflex are conducted in two fiber tracts: one in the anterior and one in the posterior column. There are also two paths for the descending impulses: the pyramidal tracts and MONAKOW's bundle. The "contact" reflex of lower animals agrees in many points with the skin reflex in man. R. P.

Birukoff, B. Zur Theorie der Galvanotaxis. *Arch. f. (Anat. u.) Physiol.*, 1904, 271-296.

Galvanotaxis a combination of two factors: a physiological (general irritability) on the one hand, and a purely physical (kataphoric action on the other. R. P.

Muskens, L. J. J. Studies on the Maintenance of the Equilibrium of Motion and its Disturbances, so-called "Forced Movements." *Jour. of Physiol.*, 1904, **31**, 204-221.

Experiments producing forced movements after lesions of the central nervous system were performed on octopods, selachians (Acanthias, Scyllium), frogs, cats and rabbits. The conclusions with reference to lower vertebrates are: 1. That rolling after unilateral lesion of the hind-brain, and circus movement after unilateral lesion of the base of the mid-brain appear to be, in lower vertebrates, fundamental phenomena, especially localized in these parts; 2. That rolling to the impaired side and circus movement to the non-impaired side are phenomena narrowly related; 3. There is no reason to believe in any diametrical opposition of forced movements of an irritating and of a paralyzing nature. In cats and rabbits unilateral lesions of the middle and upper cerebellar peduncle and unilateral (partial more than com-

plete) removal of a lateral lobe of the cerebellum cause rolling movements to the side of the lesion, or a tendency to it. The most marked rolling was observed after lesion or section of the middle peduncle. Studies on the changes in the mobility of the eyeballs were also conducted.   R. P.

Woodworth, R. S. and Sherrington, C. S. A Pseudaffective Reflex and its Spinal Path. *Jour. of Physiol.*, 1904, **31**, 234-243.

The lateral column furnishes the headward path in the spinal cord for *nociceptive* (algesic) arcs; each lateral column conveys such impulses from *both* lateral halves of the body, and somewhat preponderantly those from the crossed half; these relations are true whether the arcs be traced from skin, muscle or viscus.   R. P.

Langley, J. N. On the Question of Commissural Fibers between Nerve Cells having the Same Function and situated in the same Sympathetic Ganglion, and on the Function of Post-Ganglionic Nerve Plexuses. *Jour. of Physiol.*, 1904, **31**, 244-259.

Concludes that since pilo-motor nerve-cells, in a given ganglion of the sympathetic system can be shown not to be connected with each other by commissural fibers, and that the same is true of pupillo-dilator and vaso-motor nerve-cells, it is fair to assume "that none of the nerve-cells of the sympathetic system, and none of the similar nerve-cells on the course of the cranial and sacral nerves are so connected."

R. P.

Langley, J. N. and Anderson, H. K. The Union of Different Kinds of Nerve Fibers. *Jour. of Physiol.*, 1904, **31**, 365-391.

The nerve fibers dealt with are divisible into four classes, (a) the efferent fibers which run from the central nervous system and end in multi-nuclear striated muscle cells (efferent somatic fibers), (b) the efferent fibers which run from the central nervous system and end in ganglion cells (pre-ganglionic fibers), (c) the efferent fibers given off by the peripheral ganglia (post-ganglionic fibers) and (d) afferent fibers connected with nerve cells in the posterior root ganglia. The general conclusions drawn from the experiments are, (1) The central end of an efferent fiber can make functional connection with the peripheral end of any other efferent fiber of the same class whatever be the normal action produced by the two fibers. (2) The central end of any fiber of class (a) can make functional union with the peripheral end of any fiber of class (b), and the central end of any fiber of class (b) can make functional connection with the peripheral end of any fiber in class (a). (3) The peripheral ends of cut nerve fibers appear to have a chemotactic influence on the central ends. The chemotactic action is strong-

est among fibers of the same class. (4) It is provisionally concluded that (A) efferent fibers proceeding from the spinal cord, (B) post-ganglionic nerve fibers, and (C) afferent nerve fibers are incapable of coalescing with one another. R. P.

Robertson, T. B. On the "Sham-Death" Reflex in Spiders. *Jour. of Phys-iol.*, 1904, **31**, 410-417.

Three species of spiders were used, two classed as "active" (*Epeira producta* (?) and *Amaurobius sp.*) and one as "sluggish" (*Celae-nia excavata*). To produce the "sham-death" reflex in the active spe-cies the stimulus must be sharp and sudden. In the sluggish species the "sham-death" posture is continuous and therefore practically inde-pendent of the stimulus. The reflex is carried out without the aid of the abdominal nerves, and in the active species can be performed in an altered manner by the thoracic ganglia alone, or even by the gang-lia of the two posterior or two anterior segments of the thorax alone. In the sluggish species the reflex cannot be induced without the head ganglion. The "sham-death" reflex is a complete tetanus when the nervous system is intact. In conclusion the author says : "In the active species of spiders, in which the "sham-death" posture is prob-ably a means of escape in emergency even if they be regarded as pos-sessing "conscious volition" at all, unless we suppose that this is an attribute of each of the thoracic ganglia, this reaction cannot be *due* to their conscious volition. That is to say, purposeful as it may seem as a means of protection from their enemies, this reaction is a neces-sary consequence of the structure of their nervous system and the functional activities of the nervous elements, independently of any mental processes connected with the cerebral nervous masses."

R. P.

Langley, J. N. and Anderson, H. K. On Autogenetic Regeneration in the Nerves of the Limbs. *Jour. of Physiol.*, 1904, **31**, 418-428.

May, W. P. The Innervation of the Sphincters and Musculature of the Stom-ach. *Jour. of Physiol.*, 1904, **31**, 260-271.

Elliott, T. R. and Barclay-Smith, E. Antiperistalis and other musular Activities of the Colon. *Jour. of Physiol.*, 1904, **31**, 272-304.

Sherrington, C. S. On Certain Spinal Reflexes in the Dog. *Jour. of Physiol.*, 1904, **31**, (pp. 17-19 of Proc. Physiol. Soc.)

Stuart, T. P. A. A Contrast (?) Experiment. *Jour. Physiol.*, 1904, **31**, (pp. 6 and 7 of Proc. Physiol. Soc.)

Werndly, L. U. H. C. Aequisonore Flächen rings um eine ertönende Stimm-gabel. *Arch. f. (Anat. u.) Physiol.*, 1904, 297-304.

De Fleury, Maurice. Manuel Pour L'Etude des Maladies Du Système Nerveux. *Paris, Felix Alcan*, 1904.

This work is essentially the digest of DE FLEURY's effort to review the status of neurology after several years of special work on the neuroses. With his clearness of distinction and presentation he hoped to do a valuable service to the student by putting together the notes from his reading. The result is a volume of 1000 pages, beginning with very full directions as to how to examine a case (pp. 1-105). This is followed by a brief medical anatomy of the nervous system (pp. 109-216), very elementary and schematic, but filling its purpose for beginners. The rest of the book is devoted to the individual diseases, very concise and lucidly written. There is, of course, a great latitude of personal predilections; the chapter on neuroses is especially well treated.

As a student's manual and for rapid orientation the book deserves full praise. A. M.

Camus, Jean and Pagniez, Ph. Isolement et psychothérapie. Traitement de l'hystérie et de la neurasthènie. Pratique de la rééducation morale et physique. Préface de M. le professeur DEJERINE, médecin de la Salpêtrière. *Paris, F. Alcan*, 1904.

For a number of years Professor DEJERINE has paid attention to the method of isolation and to psycho-therapeutics in hospital and private practice.

His pupils here present a work which gives on ground of 60 well chosen observations the statement of therapeutics which they developed and extended on the ground of DEJERINE's principles. After four historical chapters, they discuss the isolation and the various forms of its application, the rest and over-feeding, and other physical helps, such as electrization and hydrotherapeutics. And after a discussion of the reciprocity of physical and mental life, they enter upon hypnotism; the comparative value of suggestion and persuasion; the importance of confidence and attention of the patient, and the means of obtaining them; and finally the rules for psycho-therapeutic conversation and the principles of reeducation.

A final chapter speaks of prophylaxis, heredity, education, and the question of overwork.

Considering the material presented, the book is an extremely valuable help in many practical and general questions concerning the neuroses. A. M.

Hall, G. Stanley. Adolescence. Its Psychology and Relation to Physiology, Anthropology, Sociology, Sex, Crime, Religion and Education. *New York, D. Appleton and Company*, 1904. Vol. I. xx + 588, Vol. II, 784 pp.

This work, by intent at least, is a biological psychology. The author has devoted many years to the study of various aspects of adolescence. During this time he has influenced and encouraged a great number of students in the investigation of problems of genetic psychology; unceasingly he has urged that "the studies of the mind need new contact with life at as many points as possible." Instead of speculating concerning the future of the soul we should study its past, if we are desirous of understanding its present condition. "We must collect states of mind, sentiments, phenomena long since lapsed, psychic facts that appear faintly and perhaps but once in a lifetime, and that in only few and rare individuals, impulses that, it may be, never anywhere arise above the threshold, but manifest themselves only in automatisms, acts, behavior, things neglected, trivial and incidental, such as DARWIN says are often most vital. We must go to school to the folk-soul, learn of criminals and defectives, animals, and in some sense go back to ARISTOTLE in rebasing psychology on biology, and realize that we know the soul best when we can best write its history in the world, and that there are no finalities save formulae of development."

The work is much more than an assemblage of facts, for the author has convictions as well as ideas. His concern, as early appears, is with the bearing of his researches upon education. A few words from the introductory remarks will serve to indicate the practical trend and tone of the book. "Never has youth been exposed to such dangers of both perversion and arrest as in our own land and day. Increasing urban life with its temptations, prematurities, sedentary occupations, and passive stimuli just when an active, objective life is most needed, early emancipation and a lessening sense for both duty and discipline. . . . ." And again, "In education our very kindergartens . . . . . tend to exterminate the naive which is the glory of childhood. Everywhere the mechanical and formal triumph over content and substance, the letter over the spirit, ... information over education, marks over edification, and method over matter."

The Psychology of Adolescence, as the book might be called, is full of the earnestness of purpose and enthusiasm of the author. Its facts are vitalized by the sense of contact with life which each page gives. President HALL has handled with admirable skill a subject which was at many points extremely difficult of treatment.

R. M. Y.

Davenport, C. B. The Collembola of Cold Spring Beach, with Special Reference to the Movements of the Poduridae. *Cold Spring Harbor Monographs,* II. 32 pp., 1 pl., 1903.

This is a description of the form, systematic relationships, habitat and modes of behavior of the simple insect *Collembola*. Apart from the new results of observation, which are interesting even to non-technical readers, the paper is valuable for its suggestions of methods and interests in the study of animals.

The spirit and purpose of the writer in his research can best be understood with the aid of the following paragraph from the monograph: "By this analysis I wish to enforce the idea that the movements of the podurids are not to be referred to so many 'volitional' acts; nor that, as instincts, are we to think of the tendency to particular kinds of behavior as having been inherited. But rather, the animal being provided with a sensitiveness of a certain sort to oxygen, to water, to currents of air or other movements, to contact, to gravity, and to light, it will behave on the beach as we see it behave there. Under another set of environmental conditions it will behave very differently. The movents of the podurids *on the beach* are the result equally of the specific, inherited capacity of response on the one hand and the particular stimuli afforded by the conditions of the beach."

And again, in a brief but effective summary the author thus states the chief matters of observation: "The podurids of the beach live between tide-marks, go into the sand at high tide and rise to the surface when the tide is out to take air. They run up surfaces in the face of the wind and leap when they reach the top, being blown back to the starting point. They are exceedingly sensitive to gravity, to contact, to moisture, to currents of air and to light, and these elementary reactions are so combined as to bring about their normal movements. They are provided with these instincts before they reach the beach. Had they not had such instincts they could never have lived on the beach. The instincts have selected the habitat."

<div align="right">R. M. Y.</div>

Bigelow, Henry B. The Sense of Hearing in the Goldfish, Carassius auratus L. *American Naturalist,* 1904, **37,** 275-284.

The experiments which form the basis of this paper were performed to test the accuracy of KREIDL's conclusions, "that goldfishes do not hear"—a conclusion reached after studying the sound reactions in fishes from which the semicircular canals with the attached parts had been removed.

The author first studied the reactions of normal fishes to sound vibrations and found that at least 78% of them gave definite well

marked reactions to such vibrations. He then studied the sound re-
actions of fishes on which various operations had been performed.

In one lot of fishes the skin was rendered insensitive by cutting
the spinal cord and the lateral branches of the 10th, 7th and 5th nerves.
The fishes with few exceptions recovered from the operations and
many of them lived for weeks afterward. 80% of the animals with
the nerves of the skin destroyed still gave normal reactions to sound
vibrations.

In a second lot the ears were made insensitive by cutting the 8th
nerves. This resulted in complete loss of response to sound vibrations.

In a third lot the 8th nerve on one side was first cut in each fish.
After this operation the fishes gave practically normal sound reactions,
but after the nerve of the opposite side had been cut the fishes no
longer responded to sound vibrations.

In a fourth lot the semicircular canals and attached portions of
the ears were pulled out. After this operation, the fishes still reacted
to sound, but the reactions were less marked in normal fishes.

The author thus repeated KREIDL's experiments and confirmed
his results, but on dissecting these fishes he found that a portion of the
ear largely imbedded in bone had not been removed. This portion
he thinks probably represents the combinrd sacculus and lagena of
higher vertebrates. It contains two otoliths and is well supplied with
nerves from a branch of the 8th.

The experiments seem to show beyond a doubt, that the ear in
goldfishes functions as an organ of hearing. A somewhat similar set
of experiments, performed a year earlier by Dr. G. H. PARKER on
Fundulus heteroclitus, led to the same conclusion with reference to that
species. Dr. PARKER, however, was unable to note any reaction to
sound vibrations in the smooth dog fish.   S. O. MAST.

Andrews, E. A. Breeding Habits of Crayfish. *American Naturalist*, 1904,
      37, 165-206.

In this paper the author describes the habits of *Cambarus affinis*
taken from the Potomac river. The habits of *C. affinis* are found to
vary considerably from those of *Astacus*, the European crayfish. This
fact lends additional interest to the observations of ANDREWS.

The most important points brought out in the paper may be
briefly stated as follows :

Mating takes place during February, March and April, and
sometimes in October and November. Each male may mate with
more than one female. Sex union continues from 2 to 10 hours. The
sperm is transferred to external seminal receptacles. The eggs are

laid at night, often not until "some weeks" after sexual union. After the eggs are laid the mortality is great among the females. It is, however, still greater among the males after sexual union, many dying immediately thereafter. Before the eggs are laid, the female thoroughly cleans her ventral surface. The eggs, from 400 to 600 in number, are fastened to the pleopods in clusters, much like bunches of grapes. Immediately after laying the eggs, the female seeks a dark place and there rolls from side to side, resting from 1 to 6 minutes on either side and on the ventral surface. This reaction continues for several hours and probably serves to fasten the eggs to the pleopods. Eggs removed from the female die unless the embryos in them are well developed. It requires from 6 to 8 weeks for the embryos to hatch, after which they remain attached to the mother continuously during the first week and part of the time during the second. After the second week they no longer return to the mother. If several mothers with embryos are in the same dish, the embryos frequently crawl onto the wrong mother. There is no evidence that the mothers recognize their own young. The embryos moult 2 days after hatching. The intervals between the following 5 moults vary from 5 to 18 days.

Practically all the observations were made in the laboratory. It is to be regretted that more work was not done in the field. Most of the descriptions are worked out in detail. These together with 10 very good figures convey a very clear conception of the habits studied and seem to show that the author made keen, thorough, careful observations. The literary merits of the paper, however, might have been improved by careful revision.　　　　　S. O. MAST.

Taverner, P. A. A Discussion of the Origin of Migration. *Auk*, 1904, **21,** 322-333.

Return of birds to the winter home is easy, that to the summer home is hard; to explain. The author discusses previous theories, and concludes that sufficient emphasis has not been placed on the fact of the great increase in the bird population at the beginning of the breeding season. In southern latitudes some birds begin to breed early; when later breeders are ready to commence they find that food has become scarce. The scarcity of food thus brought about was, Mr. TAVERNER thinks, the chief cause of birds' having commenced the habit of seeking a new home at the beginning of the breeding season.

　　　　　　　　　　　　　　　WALLACE CRAIG.

Rawitz, B. Die Unmöglichkeit der Vererbung geistiger Eigenschaften beim Menschen. *Biol. Centralbl.*, 1904, **24,** No. 12, 396-408.

RAWITZ argues vigorously against the inheritability of mental traits in man. His standpoint is that of extreme materialism.　G. W.

OBSERVATIONS ON THE SPINAL CORD OF THE EMU AND ITS SEGMENTATION.

By Irving Hardesty.

(From the Hearst Anatomical Laboratory of the University of California.)

With four figures in the text.

Some months ago a zoo in San Francisco lost by sudden death two specimens of Emu (*Dromaeus novae-hollandiae*) and the management very kindly delivered the carcasses to me within a few hours after death. The birds were immediately dissected and, with certain of the other organs, the central nervous system of each was removed and preserved in 10% formalin.

The specimens were full grown and considered of large size, being nearly as large as the adult ostrich. With the exception of the head and upper part of the neck, the bird resembles the Cassowaries; but it is larger, its neck relatively longer and it belongs to a different genus. In general size of the body it is intermediate between the *Rhea*, or South American ostrich, and the ordinary or African ostrich (*Struthio camelus*). The head, though less bare, is very similar to that of the ostrich, while most of the neck, unlike the ostrich, is covered with the long streaming plumage common to the rest of the body. The wings are even more rudimentary than those of the ostrich, being nothing more than slender stubs entirely hidden in the plumage and even void of spiny rudiments of wing feathers. Similar to the ostrich, the legs are bare but somewhat shorter in proportion than those of the ostrich and are relatively more stout, the "drumstick" being nearly as large in circumference as the thigh of a medium sized man.

The spinal cord of such an animal necessarily presents features of unique interest and preparations were made with the intention of describing it.   Meanwhile, however, the paper of STREETER ('04) appeared giving a description of the spinal cord of the ostrich and on comparison it was found that the spinal cord of the emu, in its general features, is apparently so similar to that of the ostrich that a full description of it was deemed unnecessary.   STREETER's desrcription of the one may be referred to for the most part as a description of the other.

This paper, therefore, may be limited to a few of the features presented in the spinal cord of the emu not touched upon by STREETER for the ostrich and to some further observations upon one or two points less fully treated by him.

In the lumbar enlargement alone STREETER mentions having observed a segmented appearance ("neuromeres") in the ostrich cord.   He does not refer to such as present in other localities and little more than mentions it in the lumbar region. After noting a few of the general macroscropic features of the emu cord, some attention will be given here to the appearance of evident segmental enlargements in other localities, as well as in the lumbar region.   In this respect it may differ from the spinal cord of the ostrich.

Lying in the vertebral canal, the spinal cord of the emu is surrounded by an epidural cavity which is somewhat larger in proportion than is usual in the more commonly studied mammals.   The dura mater has an unusually smooth outer surface. Between the nerve pairs of the adjacent segments it appears thicker along the ventral and ventro-lateral aspects of the cord than along the dorsal aspect, while at the levels at which the nerves are attached it appears thicker along the lateral surfaces. From a number of measurements, made later from stained sections, the thickness of the dura mater was found to vary from $87\ \mu$ to $146\ \mu$, withan average thickness of $113\ \mu$. The arachnoidea is similar in proportional thicknesss and arrangement to that usually found in the mammals.   The pia, however, is relatively thick as compared with that of the mammalian cord.   It is well defined as to its outer surface and so thick as to be easily stripped from

the specimen hardened in formalin. Measurements from the sections show its thickness to vary from 36 μ to 65 μ, with an average thickness of 53 μ. Completely fused with and continuous with the pia mater are its three ligaments. These were described by STREETER as occurring in the pia of the ostrich cord and they are remarkably well developed in that of the emu. The *ligamenta longitudinalia lateralia* course along the lateral surfaces of the cord proper in a line ventral to that along which the dorsal and ventral nerve roots approach each other (*Lll*, Figs. 2, 3 and 4). The *ligamentum longitudinale ventrale* (*Llv*, Figs. 3 and 4) is triangular or dentate in section, its apex projecting into the relatively wide *fissura mediana ventralis*. Neither of these ligaments disturbs the outer contour of the pia and can only be detected in the fresh by a slight difference in the color of the lines it occupies. The lateral ligaments appear grooved into the white substance of the cord and increase in thickness with the increase in the diameter of the cord, i. e., from the neck caudad. They appear fusiform in transverse section, thinning at the edges to become continuous with the pia. Measurements at their thickest part give an average thickness of 198 μ. All three are true ligaments, being composed almost entirely of large, well defined elastic tissue fibers with the characteristic stellate cells in transverse section, while the pia proper is composed mostly of white fibrous tissue.

In addition to the usual filaments bearing blood vessels and connecting the dura with the periosteum of the vertebral canal, there occurs along each side of the specimen and a short distance caudad to the points at which the spinal nerves penetrate the dura, a series of special supporting filaments. These *ligamenta epiduralia* occur in groups of 4 to 6 each, approximately in line, and one of them, that nearest the nerve, is always larger than the others (*Lep*, Figs. 1 and 2). In the formalin material this larger one appears whiter than the surrounding tissue, cylindrical and well defined, and microscopic examination reveals it to be a bundle of elastic fibers. Upon opening the dura these bundles along each side are found to be opposite and connected with the strongest of the *ligamenta denticulata*.

Each of the specimens possessed 48 pairs of spinal nerves, or 48 segments in its spinal cord.

In the cervical divison and for about one-third the length of the spinal cord of the emu, the spinal nerves are attached at angles inclined toward the head, or in other words, the respective intervertebral foramena through which the nerves pass are slightly more cephalad than the levels at which their dorsal and ventral roots come together on the periphery of the cord. Along the middle third of its length the nerves are attached more approximately at right angles to the axis of the cord. As in the ostrich, the spinal cord occupies the entire vertebral canal and there is no cauda equina. The sacral and coccygeal nerves are arranged so that their respective foramena are but little caudad to the points of attachment of their dorsal and ventral roots.

In consequence of the angles at which the nerves are attached to the cord, the fila radicularia of the dorsal and ventral roots of all the spinal nerves fray along the surface of the cord in both directions. The fila of each root form cephalad and caudad divisions of the root, which divisions, increasing as they course along their respective lines of insertion, approach each other and fuse to form the root (see Fig. 2, ventral root).

As to the arrangement of their fila radicularia and their angles of

Fig. 1. The 23rd and 24th segments of the spinal cord of the emu, dorsal aspect. Dura mater intact. *Nr.*—nerve roots; *Lep.*— Ligamenta epiduralia. Natural size after formalin.

attachment, the spinal nerves of the emu differ from those

of the mammals and especially man. In the human, with the exception of the first two or three cervical nerves, all the spinal nerves of the adult pass through their intervertebral foramena caudad to the levels of their attachment to the cord and all the fila of their dorsal and ventral roots are distributed cephalad. In the human fœtus the cord occupies the entire vertebral canal and the foramen of each nerve is then opposite the segment or level of the cord at which the nerve is attached, but, owing to the fact that the vertebral column grows more rapidly than the spinal cord and continues to grow after the cord has attained its adult length, the foramena become displaced caudad. The cord being attached to the encephalon, the effects of the increase in the length of the vertebræ are super-imposed so that the nerves become pulled downward and the nerve roots are necessarily drawn caudad into progressively increasing lengths till the final effect is that the conus medullaris seldom reaches lower than the upper end of the first lumbar vertebra and the whole lumbar and sacral portion of the vertebral canal contains only the resulting cauda equina. Like the ostrich, the emu may be said to have two brains, the encephalon and the "lumbar brain", or the remarkably large *intumescentia lumbalis.* The latter, necessary for the control of the chief mass of the body musculature, lies in an especially enlarged portion of the vertebral canal. Thus the two ends of the central nervous system must become mechanically fixed long before the growth of the animal is complete, and as the vertebræ increase in length the intervening portion of the spinal cord must also increase in length. This results in remarkably long segments in the cervical and thoracic regions of the spinal cord of the emu, and as compensation, explains the fact that the nerves and nerve roots are not drawn caudad instead, as they are in man. Further, between fœtal life and maturity the lower thoracic and the lumbar vertebræ of man undergo a proportionately greater gain in length than do the cervical vertebræ,[1] thus accen-

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[1] Measurements of the length of the first five cervical vertebræ and of the lumbar vertebræ of several human skeletons at birth and several adults show

tuating the drawing downward of the more caudal pairs of nerves. The young ostriches, as I have observed them on the ostrich farms of this State, appear to have necks very much shorter in proportion to the length of the body than do the adult birds, and in all probability the same is true for the emu. If this is true, then during growth the cervical vertebræ must undergo a proportionately greater gain in length than any below them, which would explain the fact that the nerves of the upper third of the cord are attached at angles slightly cephalad instead of caudad.

Another feature to be noted in the spinal nerves of the emu is that the roots and beginning portions of the lower cervical and the thoracic nerves pass from the cord dorsalward to their respective intervertebral foramena (see Fig. 1). This differs from the course of most of these spinal nerves of the mammals and means that this portion of the cord lies deeper in the bony framework about it. The small neck nerves proper are similar in this respect to the neck nerves of the mammals. As the natural result of the dorsal direction of the nerves, the nerve roots approach each other along the dorso-lateral aspect of the cord, instead of the lateral or ventro-lateral aspect (see Figs. 3 and 4).

Fig. 2. Lateral longitudinal or horizontal section of 20th segment passing at level of central canal. *D*—dura mater; *P*—pia mater; *Lep*—Ligamentum epidurale; *Lll*—ligamentum longitudinale laterale; *Llv*—ligamentum longitudinale ventrale; *Vr*—ventral root; *Fv*—fila radicularia of ventral root; *Sg*—substantia grisea; *Cc*—canalis centralis; *Nmm*—nucleus marginalis minor; *Se*—segmental enlargement; *M*—level midway between nerves. × 4. The parts were outlined by camera.

Fig. 3. *Se and M.* Transverse sections of 22nd segment. *Se*—taken through segmental enlargement corresponding to level similarly indicated in Fig. 2; *M*—taken midway between the enlargements of the adjacent segments at level similarly indicated in Fig. 2. *Llv*—ligamentum longitudinale ventrale; *Fr*—fila radicularia of both roots; other reference letters same as in Fig. 2. Outlined by camera. × 4.

Fig. 4. *Se and M*—Transverse sections of 17th segment. Taken at levels corresponding to those of Fig. 3. Reference letters, drawing and magnification same as in Fig. 3.

that between birth and the adult stages the cervical vertebræ undergo an average gain in length of about 250 %, while the lumbar vertebræ gain about 450 % in length.

Fig. 2

Fig. 3 Se

Fig. 3 M

Fig. 4 Se

Fig. 4 M
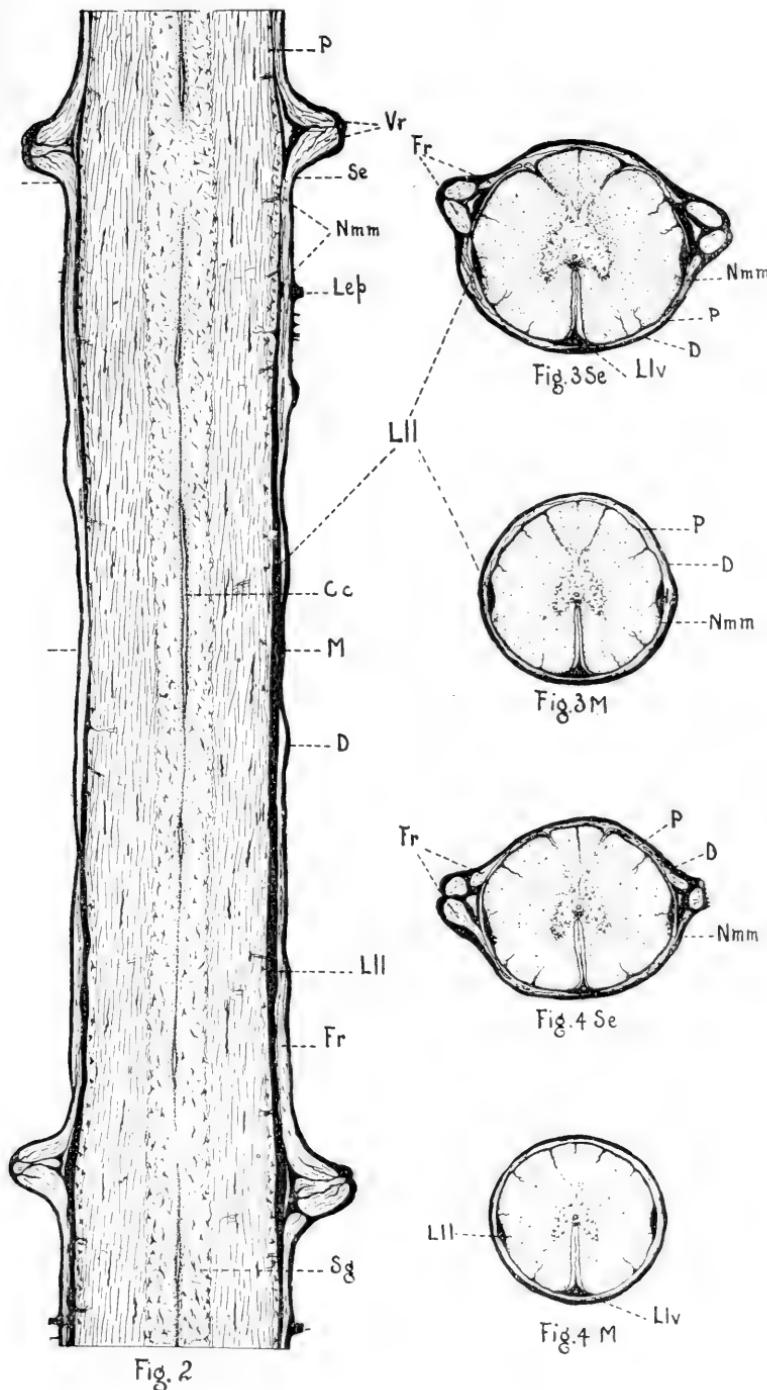
The nerves were clipped within the vertebral canal and the brain and spinal cord were removed unseparated, with the dura mater intact except that of the ventral surface of the brain· The whole was placed in 10% formalin which was renewed on the following day. No measurements were made till after the material had .been in this fluid for several months and, unfortunately, no weights were taken in the fresh condition. At the time the study began some weighings and measurements were made of the formalin material. Since the two specimens proved to be quite similar, the following record for one of them will serve for both:

Length of entire nervous system . . . . 96.5 centimeters.
Length of spinal cord from tip of calamus scriptorius
   to end of conus medullaris . . . . . 90. "
Lateral diameters of spinal cord:
    1st segment, near calamus scriptorius . 8. millimeters
    8th segment . . . . . . 5. "
    17th segment, ... 6. "
    22nd segment, ... 7. "
    32nd segment, ... 17. "
    42nd segment, ... 3. "
Weight of brain and spinal cord with dura except
   that of basal surface of brain . . . 69.5 grams.
Weight of brain severed at tip of calamus
   scriptorius . . . . 26.1 "
Weight of spinal cord from tip of calamus
   scriptorius to end of conus medullaris . . 43.3 "
Weight of lumbar region, 28th to 38th
   segments inclusive . . . . . 9.2 "

Owing to the action of the formalin upon the tissue, the weights must be regarded as ranging somewhat higher than the fresh material would have given. They may be considered as approximate however, and as indicating the relations between the parts. In every case the pieces were dried on blotting paper for a given length of time before weighing.

It will be noted (1) that the cord is quite slender, being about twice as long as that of man; (2) that the cord is relatively nearly twice as heavy as the brain, and (3) the great size of the lumbar enlargement, it being nearly one-third the weight of the brain, and measurements show it to have more than twice the diameter of any other region of the cord.

The following features should be mentioned in which the spinal cord of the emu differs from that of the ostrich, as described by Streeter:

1. The ostrich is given 51 pairs of spinal nerves or 51 segments in its spinal cord. Each of the specimens of emu here studied had but 48 segments.

2. While the sinus rhomboidalis in the dorsal aspect of the lumbar enlargement is very evident in the emu cord it is not quite so wide relatively as Streeter shows it to be in the ostrich.

3. The entire length of the spinal cord of the Emu from the point of the calamus scriptorius to the end of the conus medullaris was in one specimen 87 centimeters and in the other 90 centimeters. Practically the same measurement gave Streeter 81 centimeters for the ostrich. He mentions however that his specimen was a young one.

4. To the unaided eye there was no evidence whatever of a distinct cervical enlargement in the spinal cord of the emu. Streeter indicates an enlargement in the ostrich, evident in the gross appearance.

According to Fürbinger ('88) the 17th to the 21st segments of the ostrich cord correspond to the region of the cervical enlargement of the higher vertebrates. In the emu, as in the ostrich, the smallest part of the cord is in the neck proper—about the first twelve segments. This is to be expected from the fact that for the slender neck the inervation required of these segments must be small. At the 16th segment in the emu there begins a perceptible increase in the general diameter, in the middle of the 8th segment both the lateral and dorso-ventral diameters being 5 millimeters, while in the middle of the 17th segment, the diameter was nearly 6 millimeters. From the 16th segment a gradual increase continued till at the 22nd segment the general diameter became 7 millimeters. From the 22nd to the 27th segment, instead of a decrease there was an increase though more gradual than before. At the 27th segment the increase toward the lumbar enlargement began to show and at the 29th segment the increase became more sudden. At the 32nd

segment, which is in the height of the lumbar enlargement, the lateral diameter became 16 millimeters. The dorso-ventral diameter, however, taken along the lateral wall of the sinus rhomboidalis and the fissura ventralis, was only 7 millimeters.

From the caudal end of the first segment to the beginning of the lumbar enlargement, the spinal cord of the of the emu appears cylindrical or circular in section. With the lumbar enlargement there begins a slight lateral flattening of its contour which attains its height at the middle of the enlargement. The conus medullaris is relatively much longer than in the mammalian cord. At first the decrease from the enlargement is quite sudden, then becomes more gradual, the conus being drawn out to very slender proportions and comprising fully 10 segments, all of which are shorter than those cephalad to the lumbar region.

In length the segments of the two extremities of the cord were considerably shorter than those of the intervening portion, gradually increasing in both directions but more rapidly from the cephalic end. In the thoracic region they attained a remarkable length. The following are the lengths of some of the segments of one of the specimens obtained by measuring from the center of attachment of one nerve pair to that of the next. The measurements were made upon the formalin preserved material.

1st segment		.	.	.	.	6 millimeters
6th	"	.	.	.	.	28 "
12th	"	.		.	.	35 "
18th	"	.	.	.	.	36 "
22nd	"	.	.	.	.	38 "
26th	"	.	.	.	.	30 "
29th	"	.	.	.	.	21 "
31st	"	.	.	.	.	15 "
33rd	"	.	.	.	.	10 "
35th	"	.	.	.	.	8 "
37th	"	.	.	.	.	6 "
40th	"	.	.	.	.	5 "

STREETER ('04) described segmental swellings in the lumbar enlargement of the ostrich and shows them occurring at the level of the attachment of the ventral roots of this region.

Such swellings, though discernable, were not so marked in this region of the emu cord as his illustration shows them for the ostrich. However, in the longer segments of the emu cord there are indications of segmental arrangement not described by STREETER for the ostrich. These appear in the specimen as slight enlargements either at or, in the upper segments, just caudad to the levels at which the nerve roots pass through the dura mater. They are sufficiently evident to be easily noted in the fresh specimen both with the dura intact and after it has been removed. They are formed by a somewhat gradual increase in the diameter rather than as bulbous swellings and they are evident from the dorsal aspect as well as from the ventral and lateral views of the specimen (*Se,* Fig. 1).

The appearance is more marked before the dura is removed. This is due to the dorsal and ventral root fibers collecting beneath the dura to form the roots, as may be seen in Figure 2, which is a lateral longitudinal section passing- along the line of formation of the ventral roots. It is most apparent in the longest segments where the nerves are considerably apart, while obviously in the shorter segments it becomes less discernable or not at all, owing to the fusion of adjacent swellings.

By comparison of transverse sections through the different levels of a segment the nature of the segmental enlargements may be observed and their extent determined. Figure 3, *Se,* represents a stained transverse section taken just below the level at which the 22nd pair of nerves is attached, or the level corresponding to that indicated by *Se,* figure 2, which is a longitudinal section of the 20th segment. Figure 3, *M,* is a transverse section of the 22nd segment midway between the nerves (level *M,* fig. 2). Figure 4, *Se* and *M,* represent similar sections from the 17th segment. It is seen at once that the *Se* sections are of appreciably greater diameter than those designated by *M* and that the increase involves both diameters of the specimen. The following measurements of a few of the segments indicate the extent of the segmental enlargements. They are made from stained and mounted transverse sections and are exclusive of the dura mater.

Number of Segment.	Diameters in millimeters	
	Lateral	*Dorso-ventral*
Near tip of calamus scriptorius	10	4.
1st segment :		
near nerve	7	5
mid-way between nerves	6	5
8th segment :		
near nerve	5.5	5.5
mid-way between nerves	5	5
17th segment :		
near nerve	6	6
mid-way	5.5	5.5
22nd segment :		
near nerve	7	7
mid-way	6.5	6.5
32nd segment :		
near nerve	16	7
mid-way	16	6
40th segment :		
at nerve	4	3
mid-way	4	3

The dorso-ventral diameter of the 32nd segment includes the depth of the sinus rhomboidalis and the fissura ventralis. Between the two there is little more than the gray commissure of the lumbar cord.

Examination of the stained sections reveals that both the gray and the white substance of the cord take part in producing the segmental enlargements. Figures 3 and 4, which are camera drawings, show that that gray figure is larger at the levels nearer the fusion of the nerve roots than it is mid-way between the nerves of adjacent segments.

From both transverse and longitudinal sections (Fig. 2), it is apparent that the white substance plays a somewhat greater rôle in forming the swellings than the gray. For quite an extent midway between the adjacent nerve pairs of the longer segments there are no fila radicularia coursing upon the pia or evident beneath it. If ventral and dorsal root axones are connected with this region of the segment, as no doubt they are, they must course within the white substance, making their exit and entrance at levels nearer the levels of the respective nerve roots to which they belong. Just as the fila emerging or entering

along the pia collect rapidly in approaching from both direc-
tions to form the nerve roots of a segment, so must the axones
continued from them within the substance of the cord increase
in abundance toward the level at which the nerve roots are
formed and thus, together with their divisions and collaterals,
must they contribute to the segmental enlargement near this
level. As STREETER points out for the ostrich, the emu with
its large spinal cord must be an animal, the principal nerve con-
trol of whose body is supplied from its spinal cord segments
simply—''an animal that works chiefly with its primary appara-
tus." From the fact that, with the exception of the slender
caudal extremity, the most slender region of the cord is in the
neck, the great mass of its dorsal root axones must be of short
course. Indicated by the segmental swellings, it is very prob-
able that a large proportion of the dorsal root fibers of a seg-
ment are distributed in that segment alone, making many of the
reactions of the simple reflex character. Accordingly, the de-
scending cerebro-spinal fasciculi would be small, as must be the
case from the proportions of the cord.

As the efferent or ventral root fibers are absent along the
surface of the cord midway between the nerve pairs and begin
to emerge and collect rapidly toward the level at which the
root is formed, so the cell-bodies giving origin to these fibers
show a tendency to cluster toward the middle of the segment.
However, this clustering is not so great as might be expected.
The ventral columns maintain their shape and contain large
cells throughout the segment. For three of the longer seg-
ments counts were made of the cells contained in sections
through the segmental enlargements and in sections from mid-
way between adjacent nerve pairs. Each count involved 20
transverse sections of 30 μ thickness and included all cell-bodies
having a mean diameter of 10 μ and above. The following
gives the average number of cells per section found in each of
the two localities of these segments:

17th segment	near nerve . . .	17 cells
	midway between nerves .	15 cells
19th segment	near nerve . . .	21 cells
	midway between nerves .	18 cells
22nd segment	near nerve . . .	29 cells
	midway between nerves .	21 cells

In other words, the numbers of the larger cells found in the twenty sections (an extent of o.6 mm.) from each locality of the segments were :

	near nerve	*midway between nerves*
17th segment	341 cells	303 tells
19th segment	420 cells	365 cells
22nd segment	576 cells	432 cells

There were many cells smaller than 10 μ.   It is very probable that many of the cells having a mean diameter of 10 μ and above belong to association neurones and therefore do not give origin to ventral root fibers at all.   The largest cells and those considered as undoubtedly giving origin to efferent fibers gave mean diameters ranging from 25 to 45 μ.   These, however, while much more abundant near the nerve, were scattered throughout the segment indicating perhaps that many of the efferent fibers, being drawn toward the level at which the root is assembled, course some distance through the substance of the cord before emerging from it.   In longitudinal section most of the largest cells appear fusiform in shape with their long diameter drawn more or less parallel with the long axis of the cord.

The grouping of the cell-bodies in the gray substance is very indefinite.   The largest cells appear more abundant in the regions of the ventro-lateral and lateral groups.   Occasionally a large cell can be found lying in the beginning white substance about the lateral periphery of the gray figure.   Frequently one or two cells of the largest type occur in the base of the dorsal horns (STREETER's dorsal group) and perhaps correspond to the nucleus dorsalis or CLARKE's columns in other animals.

Throughout the entire thoracic cord and extending into the cervical region, there is found in the lateral periphery of the spinal cord of the emu a line of scattered cells representing the *nucleus marginalis minor* described for the birds and reptiles.   In the emu it is situated within and against the ventral border

of the ligamentum longitudinale laterale (*Nmm*, Figs. 2, 3 and 4). It is practically in line and continuous with the *nucleus marginalis major* of the lumbar enlargement. Its largest cells are about as large as those of the ventral horn and differ from them in apparently having fewer processes. They are similar in shape to those described by KÖLLIKER ('02) in the spinal cord of the dove. They are embedded in a thin column of gray substance more or less invaded by the surrounding medullated axones. These cells too are markedly segmental in their distribution. Midway between the nerve pairs of adjacent segments they are very sparsely scattered, being found at the rate of about one cell to every four or five sections. In the regions of the segmental enlargements the nucleus is thicker and the cells often occur two or three deep in it (see Fig. 2). Thus, this longitudinal band of cells also takes part in the segmental arrangement of the specimen.

According to SHERRINGTON ('00) this nucleus appears to have been first observed by GASKELL in the alligator in 1885. GASKELL ('88) mentions it in discussing the segmentation of the spinal cord in the Sauropsida (crocodiles and birds) and refers to it as a lateral-surface-group of cells which is as strictly metameric as the cells of the dorsal root ganglia. The nucleus was independently described by LACHI ('89) and KÖLLIKER ('01). KÖLLIKER gave it the name *Hofmann'scher Kleinkern* in distiction from the nucleus marginalis major, which he called Hofmann'scher Grosskern. In another paper KÖLLIKER ('02) makes a comparative study of these nuclei, finding them in the salamander, proteus, lizard, alligator, dove, and also represented in the spinal cord of young dogs. In the dove and the 15-day dog he shows the nuclei distinctly metameric, arranged, especially in the former, in isolated groups of cells one on either side of each segment. In the spinal cord of the emu the metameric groups are not so isolated and distinct as GASKELL and KÖLLIKER describe them in the alligator and dove, there being occasional cells scattered between the segmental enlargements.

The lumbar enlargement with its nucleus marginalis major and the slender conus medullaris are apparently quite similar

in section to those of the ostrich as described by STREETER. For this reason the description of these parts of the emu cord may be omitted here.

That the segmental enlargements are morphologically so evident in the emu cord is no doubt to some extent due to the great length of its segments. Were the segments as short relatively as they are in the mammals, the swellings would tend to merge one into the other and be less noticeable. However, it must be conceded that morphological segmentation at least is more marked in the spinal cords of birds and their relatives, the reptiles, than in the higher vertebrates. It is of interest as indicating the position of the birds in the animal scale. It is more marked in the still lower vertebrates, and in the invertebrates, the general rule is that the central nerve axis consists simply of a ganglionic chain, distinct ganglia for each body segment, while swellings opposite each pair of nerves are indicated in the early development of all vertebrates.

Segmental swellings in the spinal cords of the lower vertebrates have been long observed. LÜDERITZ ('81) notes that COLLINS described such enlargements at the levels of the attachment of the nerves in fishes as early as 1685. Later such conditions in the fishes, especially the Triglidae, have been frequently mentioned. CARUS ('14) was the first I think to discuss their functional significance. He also described them for the spinal cord of the snake. LÜDERITZ pictures segmental enlargements in the spinal cord of the ringed snake (*Tropidonotus natrix*) and also shows that such are indicated in the cervical segments of the rabbit. Further, by comparing transverse sections taken at different levels of the segments, he thought it indicated in the human spinal cord also. Numerous publications have since appeared supporting in general the views of these earlier writers.

The tendency of the ventral horn cells to cluster toward the levels at which the nerves are atached, also has a rather voluminous literature. It is of course very evident in those animals (fishes, etc.) having very marked segmental swellings. STIEDA ('68) may be mentioned among the first to study it in

the fishes and birds and CLARKE ('51) and KOLK ('59) were among the first to claim such grouping for the higher verte- brates. BIRGE ('82) calls attention to the clustering or pulling together of the ventral horn cells toward the regions of the attachment of the ventral roots of the frog cord and WALDEYER ('88) and KAISER ('91) discuss similar conditions in the cord of the gorilla and man.

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THE SELECTION OF RANDOM MOVEMENTS AS A
FACTOR IN PHOTOTAXIS.[1]

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Contributions from the Zoological Laboratory of the University of Michigan, No. 91.

It is customary to explain the phototactic movements of organisms as dependent upon a sort of forced orientation which is brought about by the fact that when the two sides of the body are stimulated unequally they give unequal muscular responses which result in turning the animal until both sides are stimulated to the same degree, when the creature moves either towards or away from the light in the direction of the rays. But however satisfactory this explanation may be for the phototactic movements of most organisms, there are several cases where locomotion is directed by the rays of light which cannot be accounted for in this way. It is well known that earthworms, leeches, and the larvæ of house-flies, blow-flies and many other insects have a strong tendency to shun the light and collect in the darkest regions they can reach. These forms have been cited as affording typical illustrations of negative phototaxis. The often precise orientation of these organisms to the direction of the rays very naturally disposes one to explain their phototactic movements as taking place according to the scheme just mentioned. No one has attempted to work out in detail the exact mode of response in any of these forms, although the fact of their orientation to the direction of the rays of light has been described by several different observers. A variety of explanations may be offered according to the gener-

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[1] The descriptive part of this paper with the exception of a few minor changes was read before the section of Animal Morphology of the International Congress of Arts and Sciences at St. Louis, Mo., Sept. 21, 1904.

al theory we have referred to. It might be assumed, in the earthworm, for instance, that light causes a greater contraction of the longitudinal muscles on the less illuminated side, or that it inhibits the action of the longitudinal muscles on the side that receives the greater stimulus, or that both these effects are combined. The attempt was made to get some clue to the method of orientation by carefully watching the movements of the animals under the influence of light. It soon developed that what seemed at first a forced orientation, the result of a direct reflex response, is not really such, but that the orientation which occurs and which is often quite definite is brought about in a more indirect manner by a mode of procedure which is in some respects similar to the method of trial and error followed by higher forms.

The response of the earthworm to light has been noted by several observers Hofmeister,[1] Darwin,[2] Graber,[3] Yung,[4] Hesse,[5] Parker and Arkin,[6] Smith,[7] and Adams.[8] While all parts of the surface of the earthworm are sensitive to light the directive influence of light, as Parker and Arkin have shown, is greatest at the anterior end of the body and diminishes towards the posterior end. The negative reaction of the earthworm becomes less as the intensity of the light is diminished, and in very weak light the reaction, according to Adams, becomes slightly positive. The directive influence of light was tested by Parker and Arkin and by Adams by placing the worm at right angles to the direction of the rays and noting the number of times it extended its head towards or away from the

[1]Hofmeister, W. Die bis jetzt bekannten Arten aus der Familie der Regenwürmer, *Braunschweig*, 1845.

[2]Darwin, C. The Formation of Vegetable Mould through the Action of Worms, with Observations of their Habits, *New York*, 1900.

[3]Graber, V. Grundlinien zur Erforschung des Helligkeits und Farbensinnes der Thiere, *Leipzig*, 1884.

[4]Yung, E. *Compt. Rend. Trav. Soc. Helv. Sci. Nat.* 1892, p. 127.

[5]Hesse, R. *Zeit. wiss. Zool.* 1896, **61**, 393.

[6]Parker and Arkin. *Am. Jour. Physiol.* 1901, **4**, 151.

[7]Smith, A. C. *Am. Jour. Physiol.*, **6**, 459.

[8]Adams, G. P. *Am. Jour. Physiol.*, **9**, 26.

light, or simply straight ahead. In all except very weak light the number of negative reactions was found to exceed the positive ones, the proportion being greater, as a rule, the more intense the illumination (ADAMS). In these investigations attention was mainly centered upon the direction of the response, the directive influence of light falling on different regions of the body, and the effect of light of different intensities. The mechism of the reaction was not especially considered.

If the earthworm is more likely to turn away from the light than towards it, it might be concluded that the light exercises a direct orienting effect upon its movements, but this does not necessarily follow. When exposed to a very strong light (the beam of a projection lantern passed through an alum cell was used) the earthworms experimented with showed the following type of reaction. The light in the first place stimulates the animal to activity, calling forth the regular movements of locomotion. Waves of contraction of the circular muscles pass from behind forward; the anterior end of the body is extended and set down; waves of contraction of the longitudinal muscles follow those of the circular ones and pull the posterior part of the body forward. As the worm crawls it frequently moves the head from side to side as if feeling its own way along. If a strong light is held in front of the worm it at first responds by a vigorous contraction of the anterior part of the body; it then swings the head from side to side, or draws it back and forth several times, and extends again. If in so doing it encounters a strong stimulus from the light a second time it draws back and tries once more. If it turns away from the light and then extends the head it may follow this up by the regular movements of locomotion. As the worm extends the head in crawling it moves it about from side to side, and if it happens to turn it towards the light it usually withdraws it and bends in a different direction. If it bends away from the light and extends, movements of locomotion follow which bring the animal farther away from the source of stimulus.

The experiments of PARKER and ARKIN show that the head of the worm in crawling is more apt to turn away from the light

as it extends than towards it. It is probable, although not expressly stated, that account was taken of the first decided turn that was made. If one watches carefully the movements of a worm that is placed at right angles to a strong beam of light it will be seen that the head frequently moves from side to side before extension takes place. These movements may be very slight and ordinarily would escape attention. There is often a similar movement during the process of extention. Frequently the head is bent over towards the light during the first part of the extension and then bent the other way and extended farther, or again it may be waved back and forth several times. Slight trial movements in all directions are continually being made. The reason why the worm makes more turns of a decided sort away from the light than towards it is largely because the little trials that bring the worm nearer the light are not followed up. Many of the turnings that would naturally be counted as negative are preceded by a slight positive turn followed by a stronger negative one. In order to ascertain whether the negative reaction was manifested at the very beginning of the response the following experiment was tried. A worm was allowed to crawl on a wet board. When it was crawling in a straight line it was quickly lowered into the beam from a projection lantern so that its body would lie at right angles to the rays. The exposure to the light was made in each case when the worm was contracted, and the first detectible movement of the head to one side noted. In the two specimens employed the first detectible turn was away from the light 27 times and towards the light 23 times. After a few extensions the worm in nearly all cases soon turned and crawled away from the light. The first detectible movement of the earthworm seems, therefore, to be nearly as likely to be towards the light as away from it. The slight preponderance of negative turns may be due to the fact that some of the smaller trial movements were overlooked, to a slight direct orienting effect of the rays, or merely to chance. A decided turning such as was probably counted in PARKER and ARKIN's experiments may represent a first trial, or a result of perhaps several very small trials. It is easy to

see that in strong illumination extensions towards the light are checked while those that bring the worm away are followed up, but this is not so obvious in light of weaker intensity. Whether the negative reaction takes place entirely by the selection of random movements is hard to determine with certainty, but there is no doubt that this factor plays a very large part in the process.

Experiments performed by Miss RHODES and myself three years ago upon the phototaxis of leeches showed that the method of orientation in these forms is, in principle, the same as that of the earthworm. When specimens of *Glossiphonia* are placed in strong light their locomotor reflexes are set in action. The mode of progression in *Glossiphonia* differs from that of the earthworm, although in certain fundamental respects the same. The anterior part of the body is extended, the mouth which acts as a sucker is attached, and then the posterior part of the body is brought forward and fastened by the sucker at its caudal end. Then the anterior part of the body extends again and the other movements follow as before. In its progress the leech frequently raises the extended anterior part of the body and waves it from side to side as if feeling its way. If the animal turns it in the direction of a strong light it is quickly withdrawn and extended again, usually in another direction. If the light is less strong it waves its head back and forth several times and sets it down away from the light; then the caudal end is brought forward, the anterior end extended and swayed about and set down still farther from the light than before. When the leech becomes negatively oriented it may crawl away from the light, like the earthworm, in a nearly straight line. The extension, withdrawal and swaying about of the anterior part of the body enable the animal to locate the direction of least stimulation, and when that is found it begins its regular movements of locomotion. Of a number of random movements in all directions only those are followed up which bring the animal out of the the undesirable situation.

The phototactic reactions of the larvæ of the *Muscidæ* have

been studied by Dr. Loeb[1] who found that these forms travel away from the light approximately in the direction of the rays. If an object was held so as to cast a shadow close to their line of locomotion the larvæ would crawl close to the margin of the shadow almost directly away from the light. Loeb remarks upon the significant fact that the oral end of these larvæ is the region of especial sensitiveness. Larvæ which crawled out of the shadow into the direct sunlight were often found to respond vigorously as soon as the anterior half or third of the body was exposed to the stronger illumination. "Das Thier hemmte seine Bewegung und bog den Kopf um, ca. 90-130° nach rechts und links. Kam dabei die Spitze des Kopfes wieder in den Schatten, so kehrte das Thier in den Schatten zurück. Geschah das aber, wie es meist der Fall war, nicht, so setzte das Thier seine Bewegung in das Sonnenlicht fort. Die Hemmung der Bewegung aber beim Uebergang aus dem Schatten in die Sonne war keine allgemeine Erscheinung. Meist gingen die Thiere ohne Versögerung aus dem Schatten in die Sonne. Dass die Lichtstrahlen, weche den Kopf treffen, wesenlich massgebend fur die Orientirung sind, geht aus folgender Beobachtung hervor: Hatte ich ein ausgewachsenes Thier auf einem Brett und schob ich das letztere so aus dem Schatten in die Sonne, dass nur der Kopf des Thieres von Sonnenlichte getroffen wurde, so stellte das Thier sofort seine Medianebene in die Richtung der Sonnenstrahlen. Brachte ich den aboralen Pol allein in's Sonnenlicht, so trat diese Orientirung nicht ein. Thiere, denen ich die vordersten Segmente am oralen Pol abgeschnitten hatte, führten auch keine Orientirungsbewegungen mehr gegen Licht aus. Auf solche vivisectorische Versuche indessen, die die Hemmung einer Reizwirkung zur Folge haben, ist wenig Gewicht ze legen" (*l. c.* p. 71). I have repeated the experiment of cutting off the heads of the larvæ but found that so much of the soft contents of the body flowed out after this operation that the larvæ made only indefinite movements and soon died, so the experiment threw no light upon the problem.

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[1] Loeb J. Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen, *Würzburg*, 1890.

Dr. LOEB does not discuss just how the rays of light orient the body of the fly larvæ, so we are left to suppose that he would adopt the same theory of orientation in this case that he has applied to other forms, although from his account of the movements of these larvæ it would almost seem that he had in mind the method of orientation that we have found to be followed by the angleworm and leech. Observations which I have made upon the phototaxis of blow-fly larvæ with the problem of orientation especially in mind soon convinced me that the movements of these forms are directed by light through following up those random movements which bring them away from the stimulus. In normal locomotion the fly larva raises the anterior third of its body, extends it and places it down upon the surface to which it adheres; then the posterior end of the body is pulled up, and the anterior end extended again, and so on. At each contraction the ventral part of the posterior portion of the body is brought forward more than the dorsal and is held in place by means of small projections on the surface while the anterior end is being extended, thus giving the larva a forward impetus. Successive waves of contraction pass from the posterior end and as they reach the anterior part of the body they extend it at the same time that it is raised. The locomotion is a sort of combination of ordinary vermicular movements and the looping movement which is found in the crawling of the larvæ of the geometrid moths. As the larva progresses the anterior part of the body is often swayed from side to side. When the head is put down, say to the right, the rest of the body is pulled along in the same direction. The source of progressive locomotion is mainly in the posterior half of the body, the anterior portion being used mainly to set the direction of movement.

When strong light is thrown on a fly larva from in front, the anterior end of the creature is drawn back, turned towards one side, and extended again. Often the head is moved back and forth several times before it is set down. Then it may set the head down when it is turned away from the light and pull the body around. If the head in moving to and fro comes into strong light it is often retracted and then extended again in some

other direction, or it may be swung back without being with-drawn. If a strong light is thrown upon a larva from one side it may swing the head either towards or away from the light. If the head is swung towards the light, it may be withdrawn or flexed in the opposite direction, or, more rarely, moved towards the light still more. If it is turned away from the light the larva usually follows up the movement by locomotion. Frequently the larva deviates considerably from a straight path, but as it continually throws the anterior end of the body about and most frequently follows up the move-ment which brings it away from the stimulus, its gen-eral direction of locomotion is away from the light. In very strong illumination the extension of the anterior part of the body away from the light is followed by a retraction, since in whatever direction it may extend it receives a strong stimulus and the larva writhes about helplessly for some time. Sooner or later, however, it follows up the right movement. Occa-sionally the larva may crawl for some distance directly towards the light, but after a time its movements carry it in the oppo-site direction. When once oriented the direction of locomotion of the larvæ is comparatively straight.

In the animals here described there is, so far I can discov-er, no forced orientation brought about by the unequal stimula-tion of the two sides of the body, but an orientation is produc-ed indirectly by following up those chance movements which bring respite from the stimulus. I do not deny that there may be an orientating tendency of the usual kind, but if there is it plays only a subordinate rôle in directing the movements of the animal. The orientation of these forms is essentially a selec-tion of favorable chance variations of action and following them up. It is a type of reaction differing from phototaxis in its typ-ical form. It does not come under the head of photopathy and it differs from JENNINGS' "motor reflex" by which many of the so-called tropic reactions are produced in the Protozoa, al-though in common with the two latter modes of response it may be considered as a form of "selection of over-produced move-ments." The light reactions of the forms studied may be inter-

preted as a resultant of two motor responses; first, the activities
of locomotion which are set up by the stimulus of the light, and
second, the act of jerking back and bending the body from side
in response to a strong stimulus from in front.   Here are two
instincts or reflexes, however we may be pleased to call them,
which are in a measure antagonistic in that the first is frequent-
ly overcome by the second.   The direction of the external stim-
ulus determines which of these two instinctive tendencies pre-
dominates.   We do not need to assume that the animal con-
sciously selects and follows up the movements that bring it out
of a disagreeable situation, and we need not assume that any as-
sociation is established between stimulus and reaction, even of
the most fleeting sort.   I do not wish to state dogmatically that
such an association is never formed in these organisms, since
observations on other forms lead me to speak guardedly on this
point; but it cannot, I believe, be more than a minor factor in
their phototactic response, if it exists,   In so far as the effect
of previous experience is not involved, the type of reaction in
question differs from the trial and error method of primitive an-
imal intelligence.   At the same time, it resembles that method
in that a multitude of movements are made of which only cer-
tain ones are followed up.   It may be said to be a form of the
trial and error method minus the element of learning by exper-
ience.

The type of reaction we have described is one which is
very widespread among the lower animals, and it doubtless en-
ters as one element into many of the tropic reactions which we
commonly explain as the result of forced reflexes.   The element
of spontaneous, undirected activity is one of vast if not essential
importance in the life of nearly all animals.   The simpler ani-
mals profit by their varied experience, although they may not
learn, and thus secure some of the advantages which it is gener-
ally considered the special function of intelligence to confer.

In a valuable paper which appeared after the preceding
portion of this article was written Dr. JENNINGS[1] points out the

[1]JENNINGS, H. S.   Contributions to the Study of the Behavior of Lower Or-
ganisms, *Washington*, 1904.

important rôle played by the method of trial and error in the behavior of the lower organisms, especially the protozoa. In the work that has been done on the instincts and reactions of animals in recent years too much stress has doubtless been laid upon the action of the environment on the organism and too little upon the internally initiated actions of the organism itself. Animals are frequently regarded as if they were more or less passive instruments played upon by external agencies and responding in the right way because they are so constructed that they cannot do otherwise. Rather, they are like instruments running by their own inherent energy, like a music box that is wound up and so regulated as to produce a variety of melodies. External agencies press the stops here and there and change the tune. If one tune does not suit, the environment is heard from and the instrument shifts to another.

The method of trial and error in its widest sense is one of those very large categories under which a multitude of varied activities may be subsumed. Even the process of natural selection may be considered a form of it, since all variations may be regarded as trials, and the unsuccessful ones errors. By a little squeezing we might also include many of the phenomena of development and regeneration. In psychology it is commonly recognized not only as the method of primitive animal intelligence, but as forming an essential element of the process of reasoning in its more abstract forms. Now it is coming to be read back into the realm of instinct and tropisms. In all these fields it is, *par excellence*, the method of adaptation. Instinctive behavior is either a direct expression of it, or, so far as instincts are stereotyped, indirectly the outcome of it through the principle of natural selection.

The rôle played by the trial and error method in the behavior of the lower organisms has, as yet, elicited but little comment, owing probably to the fact that attention has been centered more upon other features of their behavior. It may have been considered by some investigators as too obvious for remark since anyone who attentively observes the conduct of almost any of the lower animals for ten minutes can scarcely

fail to see the method exemplified. If he were watching a chick pecking at a variety of objects and giving signs of disgust when it had seized a nauseous substance he would doubtless regard the process as one of trial and error whatever name he might apply to it. A study of the conduct of much lower organisms would disclose many cases almost equally evident. The lives of most insects, crustaceans, worms, and hosts of lower invertebrate forms including even the protozoa show an amount of busy exploration that in many cases far exceeds that made by any higher animal. Throughout the animal kingdom there is obedience to the Pauline injunction, ''Prove all things; hold fast that which is good.''

The trial and error method is set off by Jennings in sharp contrast to the usual scheme of tropic reaction. ''The tropism,'' he says, ''leads nowhere; it is a fixed, final thing, like a crystal.'' And elsewhere: ''This method of trial and error, which forms the most essential feature of the behavior of these lower organisms, is in complete contrast with the tropism schema, which has long been supposed to express the essential characteristics of their behavior. The tropism was conceived as a fixed way of acting, forced upon the organism by the direct action of external agents upon its motor organs. There was no trial of the conditions; no indication of anything like what we call choice in the higher organism; the behavior was stereo-typed.'' (p. 250). If the term trial and error is used in the wide sense here employed I cannot but think that the distinction between the method so designated and the orthodox scheme of tropisms is not, after all, so wide as it at first appears. The motor reaction of *Paramecium* is certainly a fixed way of acting brought about almost inevitably by certain factors of the environment. Its behavior is certainly as stereotyped as that of any organism whose reactions are definitely known. Its reactions are ''forced movements'' in the untechnical sense of this expression, and there is no more evidence of choice in its conduct than in the contraction of a muscle; for we can scarcely speak of choice in a creature that reacts in one way to all sorts of stimuli. On the other hand the trial and error method may be ex-

tended to cover the reactions of an animal which orients itself according to the usual scheme. If an earthworm when illuminated more on one side of the body than another simply turned away, by a direct reflex, from the greater stimulus and kept on doing so until the body was brought parallel with the rays we would have a case of orientation according to the commonly accepted theory of tropisms. The creature is forced into line by unequal stimulation of the two sides of its body. When in crawling one side of the body comes to be presented to the light more than the other deviation is corrected by a direct movement away from the stimulus. Getting out of line may be regarded as an error which brings about a certain reflex that sets the animal again upon a straight course. The worm keeps in an approximately straight path because those movements (errors) which bring it out of a straight course are counteracted by a definite reflex, while those movements (successful trials) which bring the creature away from the light are followed up. It is because these errors are corrected that the orientation even according to the ordinary theory, is maintained. These deviations are as much errors as the random movements towards the light in the method of orientation that is actually followed.

The stimuli in ordinary tropisms may, however, serve to prevent errors as well as to correct them after they are made. Take an organism that orients itself by the direct method. As it swings out of line it is doing so against the influence of the unilateral stimulus which tends to turn it back during, as well as after, the trial. But the mechanism of preventing the movement and of reversing after it is made is, in this case, the same; only in proportion as the checking predominates does the random character of the movements becomes reduced. Between the behavior of an organism like an earthworm that jerks back and turns to one side when the anterior end is stimulated and that of one which turns directly when the side is presented to the stimulus there is to be sure a maked difference in behavior, but there is an underlying basis of similarity in the two cases in that in both errors are made, although they are corrected in different ways. The end result of both methods is the same, i. e.

to get the organism away from the stimulus. In the one case it is accomplished by a direct reflex, without more ado; in the other only after a considerable waste of energy in inconsequential vermiculations. In orientation according to the usual theory of tropisms errors are made in abundance ; but they are corrected in a more direct and efficient way than in the more or less haphazard method so frequently followed.

By a careful analysis of the phototaxis of *Stentor, Euglena,* and some other protozoans JENNINGS has concluced that the oritation of these forms to light takes place according to the trial and error method, and not by the method of simple forced reflexes. The reactions of *Euglena* are of especial interest since this form apparently shows a combination of both direct and indirect methods of orientation to the direction of the rays. *Euglena* may react to a strong or sudden stimulus from the light by backing off and starting ahead in a new direction. Several trials of this kind may be made until finally the creature becomes oriented when it swims to or from the light according to the intensity of the stimulus. *Euglena* is also capable of orienting itself by gradually bending its course until it comes to be approximately parallel with the rays. Ordinarily this form swims in a straight spiral path. Should light shine on the body from one side the sensitive anterior end would be stimulated differently in different parts of its spiral course. According to JENNINGS, it is the diminution of light as the animal turns the anterior end away from the stimulus that causes the motor response. When the *Euglena* turns so that the anterior end is less illuminated, it is stimulated to swerve back further towards the light, and, by a succession of such responses, it finally becomes oriented to the direction of the rays. Swimming through that portion of its spiral course that causes the diminution of light at the anterior end is that part of the creatures activities that must be looked upon as error, if we go so far as to regard the passing through different sections of a continuous spiral course as trials. But to view the matter in this way is to go far towards obliterating the distinction between orientation through trial and error and orientation by the direct method. In the mode of photo-

tactic response here considered *Euglena* does not react by a number of indiscriminate movements until the right one is accidentally hit upon, but by a direct reflex whose effect is to bring the organism more nearly parallel to the direction of the rays. The phototaxis of *Euglena* is not so manifestly the outcome of the trial and error method as that of the earthworm. In the latter case light does not cause directly a movement which makes for orientation. The direct response may or may not have that effect. The successful movement is accidentally hit upon, but one can scarcely say this in the case of *Euglena* in which the orientation takes place more nearly in accordance with the usual scheme.

It is perhaps difficult to decide where best to draw the line as regards the employment of the expression trial and error. If it is extended to include the phototaxis of *Euglena* and other protozoa where there is a gradual adjustment of the path by appropriate direct responses until it coincides with the direction of the rays, we can hardly stop short of including, at least to a considerable degree, the cases of phototaxis that take place according to the commonly accepted theory. We may regard all departures from the straight and narrow path as errors according to whatever theory of phototaxis we may choose to adopt, and we can look upon all movements in that path as successful experiments. I would suggest that if the term trial and error is widened, as seems desirable, so as to include such reactions as are described in the first part of this paper where there is no discernible element of learning involved, its application be limited to those cases in which the adapted movements may be regarded as chance successes. This would exclude the tropisms of the orthodox kind; it would exclude the gradual orientation of such forms as *Euglena* where oblique stimulation causes a direct response which brings the body more nearly parallel to the rays. It would include many of the reactions of the protozoa where, as in the phototaxis of the blue *Stentor*, the right direction of movement is hit upon by chance, and a large part of the actions of higher forms. All organisms make errors. In some cases these errors are rectified by an appropriate direct reflex,

in others by the chance success of a random movement. There will doubtless occur many cases difficult to classify where trials are not perfectly random movements but where the stimulus may have a certain directive effect which is in large measure obscured. A tropism of the direct sort is not necessarily a perfectly fixed and rigid affair. It may be a tendency more or les obscured by a lot of random movements arising from internal causes. An organism may be drawn to a certain point through a direct orienting reflex, but if there be at the same time a large element of random activity in its behavior it may seem to reach that point by the method of trial and error. In the trial and error method the random character of the movements impresses us most; in the tropisms, the element of direct determination by the environment. Both of these factors run through the behavior of all animals, but they are mingled in various proportions in different forms. In the lives of most, if not all, animals both are essential elements in the adjustment of the organism to its conditions of existence.

University of Michigan, Ann Arbor, Mich., Dec. 6, 1904.

NOTES ON THE DEVELOPMENT OF THE SYMPA-
THETIC NERVOUS SYSTEM IN THE
COMMON TOAD.[1]

By WALTER C. JONES, M.D.

With twelve figures.

The work which forms the basis of this paper was done in
1898-1900, at the Zoölogical Laboratory of Northwestern Uni-
versity, Evanston, Illinois, and was presented in part fulfillment
for the degree of Master of Arts. Circumstances prevented the
immediate preparation of the results for publication. In the
considerable interval to the present, only one paper, as far as I
know, has been published, dealing with the development of the
sympathetic nervous system; this paper, by HOFFMANN, 1902,
is briefly noticed in my review of the literature. The writer
wishes to thank Professor WM. A. LOCY, Director of the Lab-
oratory, for invaluable help in the work and in the revision of
the manuscript.

The earlier view in regard to the origin of the sympathetic nerv-
ous system was that advanced by REMAK, to the effect that it arose *in
situ* from the mesoblast. BALFOUR, after his researches on elasmo-
branch fishes ('78), brought forward a new view, namely, that the sym
pathetic nervous system arises from the epiblast in connection with the
spinal and with certain of the cranial nerves. He claimed that the sym-
pathetic ganglia of the trunk region "are at first simply swellings on
the main branches of the spinal nerves." Subsequently, these swell-
ings are removed each from its respective nerve, retaining, however,
fibrous connections with the nerve through a short branch, which forms
a *ramus communicans*. They appear at first to be independent, becom-
ing united later by commissures, and forming a continuous cord on ei-
ther side.

SCHENK and BIRDSELL published, in 1879, the results of their observations on certain mammalia, which, as BALFOUR says, "seem to indicate that the main parts of the sympathetic system arise in continuity with the posterior spinal ganglia; they also show that in the neck and other parts the sympathetic cords arise as a continuous ganglionic chain."[1] ONODI ('86), working on elasmobranchs, agrees essentially with BALFOUR, and gives excellently clear figures intended to show that the cells which form the sympathetic cord arise as outgrowths from the spinal ganglia.

PATERSON, in 1891, revived the idea of the mesoblastic origin of the sympathetic nervous system. According to his researches on mouse, rat, and human embryos, the earliest traces of the sympathetic are seen as a cellular cord lying in the mesoblast between the aorta and the cardinal vein, in the anterior dorsal region. This cord is bilaterally symmetrical, and is composed of cells which he claims are differentiated mesoblastic cells. At the time of its appearance, the cord has no connection whatever with the spinal nerves nor ganglia, and constitutes the anlage of the sympathetic. The next step is the formation of the rami communicantes, which arise as fibrous outgrowths passing from the spinal nerves to the sympathetic cord. The ganglia appear next, and are formed at the points where the rami join the cord, resulting presumably from the growth of both sympathetic cells and nerve fibers. The collateral sympathetic is developed by the outgrowth from the sympathetic cord of cellular branches, which later give rise to the ganglia, nerves, and plexuses. In this category are placed the cervical and sacral portions of the sympathetic chain and also rather doubtfully, the grey rami communicantes. This view is repeated by PATERSON, in 1903, in Cunningham's Anatomy.

MARSHALL ('93), on the other hand, agrees very closely with the theory advanced by BALFOUR. In frog and chick embryos, MARSHALL finds that the sympatetic nervous system arises "as a series of outgrowths from certain of the cranial and from all of the spinal nerves. These develop ganglionic swellings,"[2] which later become connected by fibrous commissures, thus forming the gangliated chain of the adult.

HIS, Jr. ('97), tracing in the chick the history of an anlage similar to that described by PATERSON, finds, in very early stages, that the cells forming it come from the ganglia of the spinal nerves, thus confirming

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[1] *"Comparative Embryology."* Vol. *2*, p. *384*.

[2] *"Vertebrate Embryology."* Page *134*.

the researches of ONODI ('86), on elasmobranchs. In the human embryo, HIS, Jr. finds that the development of the sympathetic begins (in a 10 mm. embryo) with the outgrowth of the white rami communicantes from the spinal nerves. A little later, the sympathetic cord appears and is joined by the rami. These findings contrast with those of PATERSON ('91), who observed that the structure first to appear is the sympathetic cord, the rami developing later.

HOFFMANN'S observations on the sympathetic system of selachians ('99) agree, as far as essential features of development are concerned, with those of BALFOUR and ONODI. Like them, he shows that the cells forming the sympathetic anlage arise in connection with the spinal nerves, thus favoring the view that the sympathetic is epiblastic in origin. In urodeles, he finds ('02) the first trace of the sympathetic occurring as scattered cells connected by slender rami to the ventral branches of the spinal nerves. He does not express an opinion as to whether these cells are of epiblastic or mesoblastic origin. In 30 mm. salamanders, the sympathetic has come to be a continuous chain, in some places fibrous, in other places cellular in character, extending from the first spinal nerve back to the tail region and connected by rami to all of the spinal nerves.

Another question relates to the connection, during embryonic stages, between the sympathetic anlage and the adrenals. These two structures come into very intimate relation with each other during their development. In reptiles, there arises on each side of the vena cava soon after its formation a longitudinal cord of cells, which MINOT calls the "mesenchymal anlage" of the adrenals. On the dorsal side of this anlage and somewhat toward the median line, appear clusters of cells, which are derived from the sympathetic ganglia. They constitute the "sympathetic anlage"[1] of the adrenals.

These two portions come in contact, and at first, in amniota at least, the sympathetic part grows more rapidly, and partially surrounds the mesenchymal portion; but soon the relations become reversed, and the mesenchymal portion gradually surrounds the sympathetic; what finally becomes of the latter is not known. BALFOUR ('78) found in elasmobranchs, in the case of the posterior adrenals, that each of these bodies shows a small sympathetic ganglion attached to either end of it, the whole structure being attached to a spinal nerve by a ramus. This mass of cells gradually becomes divided into a ganglionic and a glandular portion; the latter acquiring a mesoblastic investment becomes adrenal, while the former develops into sympathetic tissue. HOFF-

[1] *"Human Embryology."* Pages 485 and 486.

MANN ('99), working on selachians, confirms the findings of BALFOUR, in their essential features.

A brief summary of the literature embodies the following points: (1) The cells from which the sympathetic arises, probably come originally from the spinal ganglia, as shown particularly by BALFOUR ('78), SCHENK and BIRDSELL ('79), ONODI ('86), and HIS, Jr. ('97), PATERSON ('91) being the most recent investigator to hold to the mesoblastic theory. (2) In elasmobranchs, the sympathetic begins with the development of the ganglia, which arise as cellular outgrowths on the spinal nerves. These gradually are removed from the nerves, retaining, however, fibrous connections, which constitute the rami The commissures arise later, probably as outgrowths from the sympathetic ganglia. (3) In mammalia and in aves, the sympathetic appears first as a continuous longitudinal cord, which later is joined by rami communicantes, arising as outgrowths from the spinal nerves. At the points where the rami join the cord, ganglia develop, while the intervening portions of the cord remain as commissures. (4) The collateral sympathetic arises as outgrowths from the sympathetic cord. (5) A portion of the sympathetic anlage has, during its development, very intimate relation with the adrenals. (6) From an embryological as well as from an adult morphological and physiological stand-point, the sympathetic system is best considered as an integral part of the whole nervous system and not as a structure that is to any considerable extent distinct or separable from the rest of the nervous system.

My own observations upon the development of the sympathetic nervous system have been confined mainly to the derivations of the ganglia, their commissures, and the rami communicantes. The observations were made upon toad and frog embryos, and were limited to the region posterior to the vagus ganglion. Graphic reconstructions were made from serial transverse paraffine sections, supplemented by actual dissections. For the sake of clearness, a general statement is given before proceeding to the description of particular stages of development:

(1) The sympathetic system between the vagus ganglion and the second spinal nerve, in the animals studied, appears to arise from cells scattered in the mesoblast of the region where the future sympathetic cord is to lie. A portion of these cells gradually becomes aggregated to form a cord (Fig's. 2, 7, and

8, *Sy.*) which is the beginning of the sympathetic as an anatom-
ically distinct structure in this region. Scattered cells are to
be seen among the fibers of the first and second spinal nerves,
all the way up to the spinal ganglia. These cells become con-
tinuous below with the cells of the forming sympathetic cord.
Also, there is a connection between the sympathetic cord in
front of the second nerve and the group of cells which give rise
to the sympathetic in the trunk region. These facts of observa-
tion favor the view that the cells which enter into the formation
of the sympathetic cord anterior to the second spinal nerve mi-
grate either (a) downward from the ganglia of the first and sec-
ond spinal nerves or (b) forward from the structure which gives
rise to the sympathetic of the trunk region, posterior to the
second spinal nerve. However, the question of the origin of
these cells requires further investigation.

(2) My preparations show that all of the sympathetic pos-
terior to the second spinal nerve arises from an antecedent
structure, which is bilaterally symmetrical, and lies closely ap-
plied to the dorsal and external side of the aorta, where the lat-
ter is double, and to the outer side of the median aorta, after
the union of the two trunks. This antecedent structure con-
sists of an irregular ridge of cells (Fig. 1, *Ri.*) extending back
to the region between the ninth and tenth nerves (Fig. 7, *Ri.*),
suffering interruption, however, in the region of the third.
Throughout its entire extent, this ridge is continuous inferiorly
with a mass of cells (Fig. 1, *Ma.*), which, between the second
nerve and the anterior end of the kidney, lies between the aorta
and the Wolffian duct (Fig's. 1, 3, 4, and 5, *Ma.*) and, in the
region of the kidney, between this organ and the aorta (Fig. 6,
Ma.). It extends some distance anterior to the second nerve,
where, however, its connection with the sympathetic is uncertain.
This ridge (Fig. 8, *Ri.*) is continuous anteriorly with the sym-
pathetic cord between the vagus ganglion and the second spin-
al nerve, and arises at the same time as this portion of the cord.
The division of the forming sympathetic into a portion anterior
to the second spinal nerve and one posterior to it is observed
throughout the following descriptions.

Nine Millimeter Stage.—Between the vagus ganglion and the second spinal nerve, at this stage, sympathetic cells are seen scattered in the mesoblast dorsal and internal to the aorta (double).   These cells are round or slightly elliptical in shape, have a granular appearance, and are devoid of processes; they stain a little more deeply than connective tissue cells, and usually are very easily distinguished from them.   At places, espe-
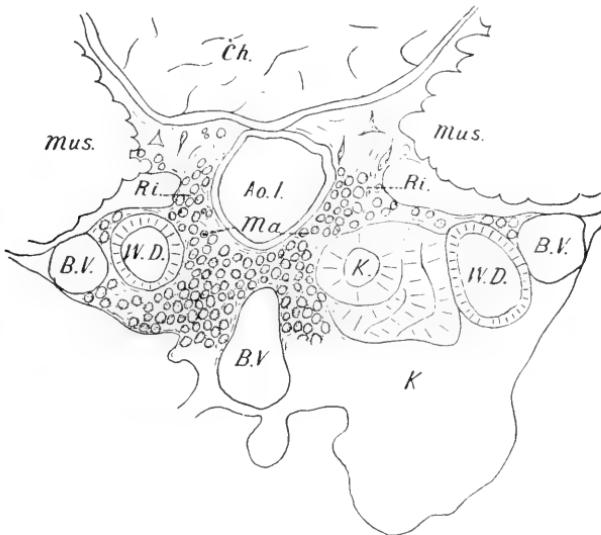
Fig. *1.*—Transverse section of 9 mm. toad, through the ganglion of the sixth spinal nerve (see Fig. 7), showing the sympathetic ridge, *Ri.* (The section passes through the extreme anterior end of the kidney on one side and just anterior to the kidney on the opposite side.)   *Ao. 1.*, Aorta (median dorsal).   *B. V.*, blood-vessel.   *Ch.*, notochord.   *K.*, kidney.   *Ma.*, mass of cells between aorta and kidney or aorta and Wolffian duct.   *Mus.*, muscle.   *Ri.*, sympathetic ridge. *W. D.*, Wolffian duct.   × 246.   Camera Lucida.   Reichert, oc. 2, obj. 7 a.

cially in the immediate region of the first and second nerves, these cells are becoming aggregated to form a cord (Fig. 7, *Sy.*), which, in cross section, appears very irregular, and shows from three to twelve cells in one section.   (Fig. 2, *Sy.* shows a little later stage.)   *This cord is the beginning of the differentiation of the sympathetic in this region.*   It becomes continuous back of the second nerve with the ridge already mentioned.

The mass of cells between the aorta and the Wolffian duct

(Fig's. 1 and 7, *Ma.*) with which the sympathetic ridge is close-
ly connected, is rather small and ill-defined anteriorly. In the
region of the fourth nerve, however, it becomes more distinct
(Fig. 7), and gradually increases in size from here back to the
anterior end of the kidney, where it lies in contact externally
with this organ instead of the Wolffian duct. Fig. 1, *Ma.*
shows this mass of cells. Between the aorta (*Ao. 1.*) and the
Wolffian duct (*W. D.*), on the left side, it represents the con-
dition anterior to the kidney; between the aorta (*Ao. 1.*) and
the kidney (*K.*), on the right side, it shows the condition in the
region of the kidney.

Midway between the third and fourth nerves, a few cells ly-
ing close against the side of the aorta are seen to form a rather
poorly defined ridge (Fig. 1, *Ri.*), which can be traced back
without interruption to the region between the ninth and tenth
nerves (Fig. 7, *Ri.*). It has not yet made its appearance in the
region of the third nerve, but traces of it are seen immediately
behind the second. *The cells of this ridge-like elevation consti-
tute the earliest structure to which I have traced the sympathetic sys-
tem in the region posterior to the second spinal nerve.* The source
of the cells constituting the sympathetic back of the second spin-
al nerve is still uncertain. I have no definite clue as to their
origin, outside of the fact that these cells mingle freely with the
nerve fibers as far back as the ninth. This close connection be-
tween the nerves and the sympathetic ridge suggests, at any
rate, that the cells are of epiblastic origin.

At this stage, then, the following points are especially to
be noted: (1) Between the vagus ganglion and the second
nerve, scattered cells are becoming aggregated to form the sym-
pathetic cord (Fig. 8, *Sy.*). (2) In the region posterior to the
second nerve, the ridge-like structure from which the sympathe-
tic arises (Fig's. 1 and 7, *Ri.*) extends from the second nerve back
to the region between the ninth and the tenth, being interrupted
in the region of the third. (3) The cells of the forming sympa-
thetic mingle freely with the fibers of the first nine spinal nerves.

Twelve Millimeter Stage.—In this embryo, between the
vagus ganglion and the second spinal nerve, we find the sympa-

thetic occurring as an almost unbroken rod of cells (Fig's. 2 and 8, *Sy.*).

Behind the second nerve, the sympathetic ridge is much higher and much better defined than in the preceding stage;
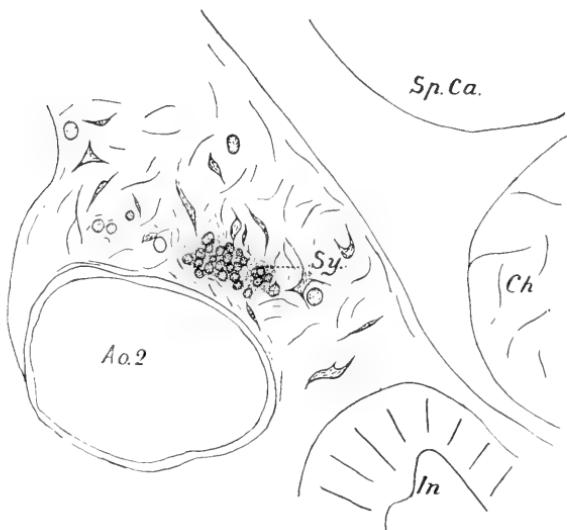
Fig. 2.—Transverse section through a 12.5 mm. toad, midway between the first and second spinal nerve (see Fig. 8), showing cells becoming aggregated to form the sympathetic cord, (*Sy.*). *Ao. 2.*, aorta (of one side, where double). *Ch.*, notochord. *In.*, intestine. *Sp. Ca.*, spinal canal. × 246. Camera lucida. Reichart, oc. 2, obj. 7 a.

the outer cells of it are becoming more closely compacted and, in some places, a definitely limiting membrane has been differentiated. *This group of cells is the beginning of the differentiation of the sympathetic cord in the body region.* In some places, this cord includes a part or all of the ridge, this being especially noticeable anteriorly, just in front of the point where the median dorsal aorta begins (Fig. 8, *). Fig. 3 is taken in this region, and shows nearly the whole of the ridge being formed into the sympathetic cord (*Sy.*).

The cellular structure with which the sympathetic ridge is connected, remains the same as in the preceding stage, except for a general increase in size and an enlargement, in the region of the fourth nerve (cf. Fig's. 7 and 8, *Ma.*). This enlarge-

ment persists in later stages, being distinctly noticeable in 18 mm. embryos, and is due to relationship with another structure, this relation suggesting that between the sympathetic and the adrenals described by MINOT.[1] The relation of the spinal nerves to the developing sympathetic system is practically the same as in the 9 mm. stage, except in the case of the sixth, where the cord is somewhat removed from the nerve, retaining distinctly, however, short fibrous connections. These fibers constitute the beginning of a ramus communicans (Fig. 8, *R.*).
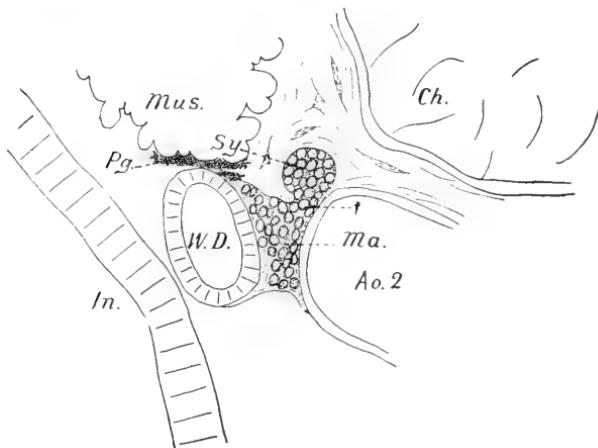
Fig. 3.—Transverse section of a 12.5 mm. toad, between the third and fourth spinal nerves (see Fig. 8), showing nearly the whole of the sympathetic ridge being transformed into the sympathetic cord, *Sy. Pg.*, pigment. Cf. neck of cells marked † with Fig. 5, *Ri.* Other abbreviations, same as in Fig's. 1 and 2. × 246. Camera lucida. Reichert, oc. 2, obj. 7 a.

Fourteen Millimeter Stage.—At this stage, the sympathetic cord is easily traced between the second spinal nerve and the vagus ganglion, except immediately behind the first nerve (Fig. 9, *Sy.*); connection with the vagus ganglion is uncertain.

Posterior to the second nerve, the ridge now has become much more prominent. In many places, it becomes high and narrow (Fig's. 6 and 10, *Ri.*) before the sympathetic cord is differentiated at the free border of it (Fig's. 5 and 6, *Ri.* and *Sy.*).

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[1]"Human Embryology." Pages 485-489.

In other regions, the cord is seen very early, including the greater part of the ridge (Fig. 3, *Sy.*), and appears to be pushed outward and upward by the ridge, as the latter becomes better developed; while more frequently the cord is not seen distinctly till the ridge has grown to about half the size to which it finally attains. Between the second nerve and the point where the median dorsal aorta begins (Fig. 9, *), the ridge lies against the aorta (Fig. 5, *Ri.*). In the region of the kidneys, it extends outward and upward, lying between this organ and
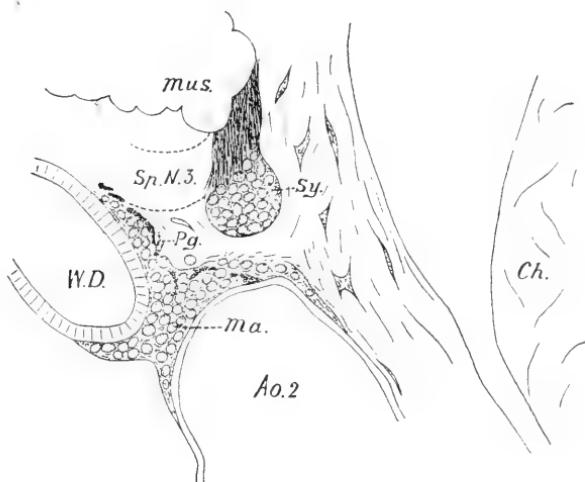
Fig. 4.—Transverse section of an 18.5 mm. toad, through the third spinal nerve (see Fig. 10), showing the relation between the sympathetic cord, *Sy.*, and the third spinal nerve, *Sp. N. 3.* The dotted parallel lines indicate the nerve as reconstructed from sections just anterior to the one here represented. For development of ramus, cf. Fig. 12. Other reference marks, same as in preceding figures. ×246. Camera lucida. Reichert, oc. 2, obj. 7 a.

the notochord (Fig. 6, *Ri.*). In the structure with which the sympathetic ridge is connected (Fig. 9, *Ma.*), two changes need to be noted ; first, a general increase in size and second, the obscuring of the sympathetic ridge in the region of the fourth nerve, due to relationship with a structure referred to in the preceding stage as being possibly adrenal.

In regard to the relation between the spinal nerves and the sympathetic, we find short rami in connection with the fourth,

fifth, sixth, and seventh nerves and an incipient one on the eighth (Fig. 9, *R.*). The relations of the other nerves are the same as in the preceding stage, except that the cord is better defined now, and, in section, has the appearance of lying against the nerve, there being fewer cells scattered among the nerve fibers. (Fig. 4, *Sy.* shows a little later stage.) At this stage, a membrane is found in many places, entirely surrounding the cord and making it perfectly distinct. We can distinguish now clearly for the first time two regions where the develop-
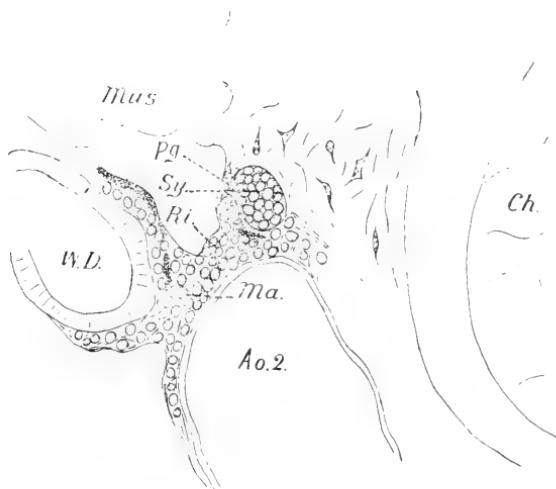
Fig. 5.—Transverse section through an 18.5 mm. toad, just posterior to the third spinal nerve (see Fig. 10), showing the sympathetic ridge, *Ri.*, and the sympathetic cord, *Sy.*, well differentiated along the free border of the ridge. Reference marks, same as in preceding figures. × 246. Camera lucida. Reichert, oc. 2, obj. 7 a.

ment of the sympathetic as a whole has proceeded father than elsewhere. These places are in the region of the brachial and the lumbar plexuses. Also, the sympathetic is usually better developed in the immediate region of the nerves than it is between them (Fig. 9).

Eighteen Millimeter Stage.—Between the vagus ganglion and the second nerve, the sympathetic is easily traced as a large, distinct, and continuous cord (Fig. 10, *Sy.*). Posterior to the second spinal nerve, the ridge (Fig's. 5 and 6, *Ri.*) now is well

marked, especially in the region of the lumbar plexus, where it has reached the height of its development (Fig. 10, *Ri.*). The angle which it makes with the horizontal plane varies in different regions. Anteriorly, it extends upward and inward (Fig. 5, *Ri.*), approaching even a horizontal position in some places. Following it backward, in the region where the median aorta begins (Fig's. 10 and 11, *), it assumes rather abruptly a vertical position, and then immediately begins to lean outward, till, in the region of the kidney, it points upward and outward (Fig. 6, *Ri.*), making an angle with the horizontal plane varying from 30° to 60°.
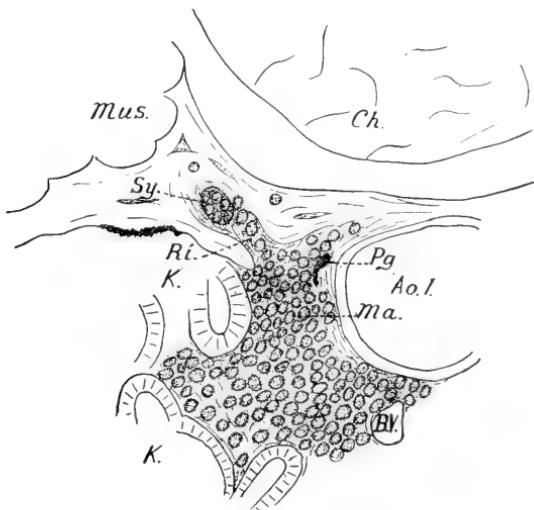
Fig. 6.—Transverse section of 18.5 mm. toad, between the sixth and seventh spinal nerves (see Fig. 10), showing the sympathetic ridge, *Ri.*, and the sympathetic cord, *Sy.*, well differentiated at the top of the ridge. Abbreviations, same as in preceding figures. × 246. Camera lucida. Reichert, oc. 2, obj. 7 a.

The sympathetic cord (Fig. 6, *Sy.*) is larger and more definite, and is found surrounded by a membrane more frequently than it is seen without one. The cord lies at the top of the ridge, including in a few places the greater part of the latter. The rami communicantes, at this stage, have increased in size and distinctness. Besides those in connection with the fourth,

fifth, sixth, seventh, and eighth nerves, there is also an incipient one on the ninth.

Twenty-one Millimeter Stage.—In a toad 21 mm. long, the sympathetic cord is continuous from the vagus ganglion back to the region between the ninth and tenth nerves. But it is to be borne in mind that the development back of the second nerve is different from that in front of this point. The ridge has mostly disappeared. A considerable portion of it remains, however, between the fourth and fifth nerves and smaller parts, posteriorly. Compare Fig. 10, *Ri.*, where the ridge is well developed, with Fig. 11, *Ri.*, in the region of the eighth and ninth nerves, where the ridge has almost completely disappeared.

Between the vagus ganglion and the second spinal nerve, the sympathetic cord is removed a considerable distance dorsally from the aorta. (Cf. Fig. 2, *Sy.*, where it lies almost upon the aorta, *Ao. 2.*) The mass of cells anterior to the kidney, with which the ridge was connected in earlier stages (Fig's. 1 and 7, *Ma.*), is still present, but is flattened posteriorly, where it occurs as a horizontal plate-like mass of cells extending laterally from the aorta. As the ridge disappears, the sympathetic cord is left alone, large and distinct, lying most of the way upon this mass of cells but not continuous with it and removed laterally a considerable distance from the aorta. In the region of the kidney, the cords lies on the dorsal side of this organ. The sympathetic cords of the two sides can be traced back as far as a point midway between the ninth and tenth nerves, where they unite underneath the aorta.

Beginnings of rami are found in connection with the first and third nerves ; a small one is seen on the second, while rather distinct ones appear on the fourth, fifth. sixth, seventh, eighth, and ninth nerves (Fig. 11, *R.*). The sympathetic cord is surrounded by a well-developed membrane, throughout most of its extent. The cord is composed now not of cells alone, for most of the way it shows fibrous structure also. Furthermore, it is better developed in the immediate region of the nerves than it is between them (Fig. 11, *Sy.*), a condition only slightly noticeable in earlier stages. Between the nerves, the cord is rela-
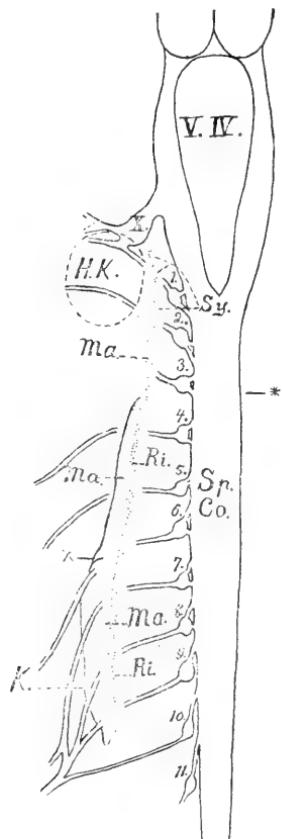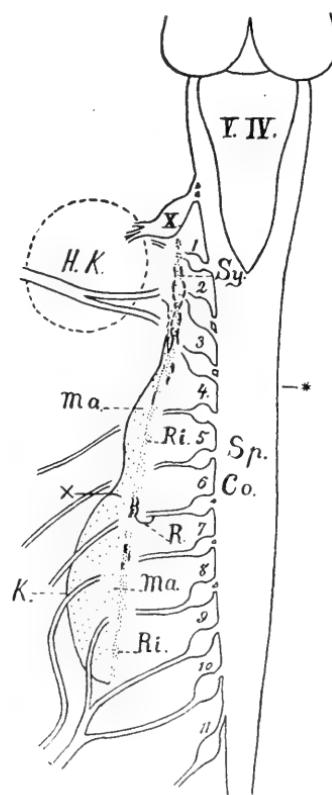
FIG. 7   FIG. 8

Fig. 7.—Diagrammatic reconstruction of the sympathetic nervous system of a 9 mm. toad, dorsal view. The kidney and the sympathetic with its related structures are represented as having been shifted from a position inferiorly along side the aorta (see Fig. 1) to a position on a level with the spinal cord, but removed laterally a distance equal to that between the sympathetic and the spinal cord before the change of position. The more closely dotted portion represents sympathetic tissue; posterior to the second spinal nerve, the *width* of this closely dotted portion represents the *height* of the sympathetic ridge. The lightly dotted area represents the structures with which the sympathetic is connected during its development. ✕ marks the anterior end of the adult kidney. The connection between the sympathetic and the spinal nerves is not shown. * marks the anterior end of the median dorsal aorta. *H. K.*, head kidney. *V. IV.*, fourth ventricle. *X.*, vagus ganglion. *1., 2.*, etc., ganglia of first, second, etc. spinal nerves. For other abbreviations, see Fig's. 1-6. ✕ 21.

Fig 8.— Diagrammatic reconstruction of the sympathetic nervous system of a 12.5 mm. toad. The representation of the rami communicantes here and in succeeding figures is exceedingly diagrammatic. For abbreviations and other explanations, see Fig. 7. ✕ 28.
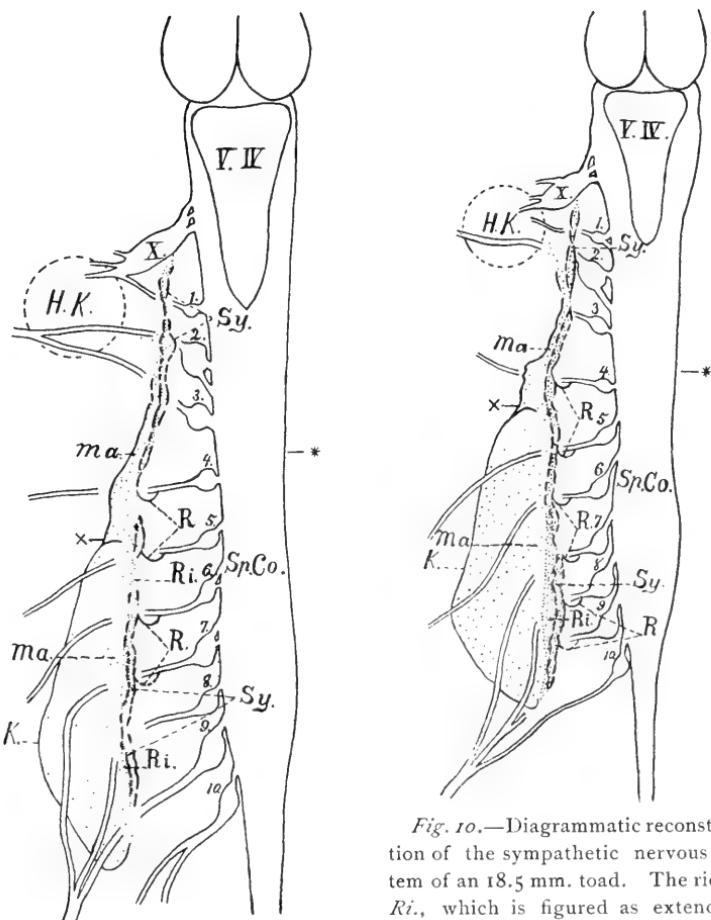
Fig. 9.—Diagrammatic reconstruction of the sympathetic nervous system of a 14 mm. toad. *R.*, ramus communicans ; dotted line lettered *R.*, ramus only partially developed. Other abbreviations, same as in Fig's. 7 and 8. × 28.

Fig. 10.—Diagrammatic reconstruction of the sympathetic nervous system of an 18.5 mm. toad. The ridge, *Ri.*, which is figured as extending inward horizontally throughout its entire extent has, in the actual specimen, an upward and *inward* direction anteriorly (see Fig. 5, *Ri.*) and an upward and *outward* direction posteriorly (see Fig. 6, *Ri.*). Reference marks, same as in Fig's. 7, 8, and 9. × 24.

tively slender, this condition being especially marked in the region of the kidney. The cellular enlargements of the sympathetic cord in connection with the nerves now may be called ganglia, and the constricted portions between the nerves, which are becoming distinctly fibrous in structure, may be called commissures.
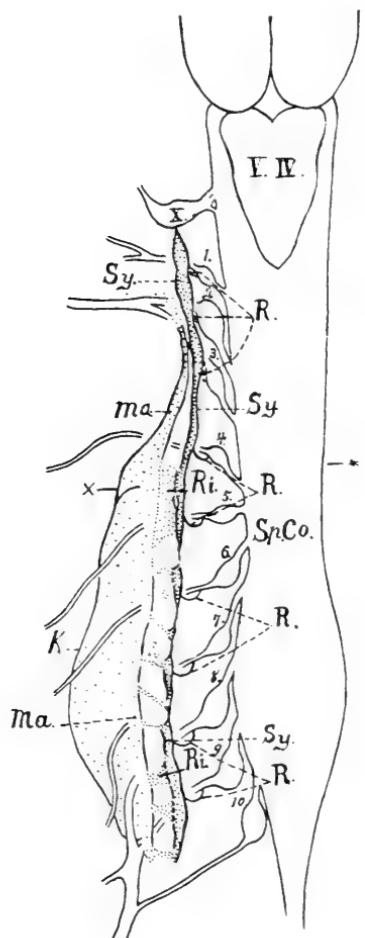
Fig. 11.—Diagrammatic reconstruction of the sympathetic nervous system of a 21 mm. toad. Reference marks, same as in previous figures. × 24.

Condition after the Metamorphosis.—By the time the tail has almost disappeared, the sympathetic cord not only is completely separated from its antecedent structures, but is removed dorsally and somewhat laterally from the aorta. In the mid-trunk region, it lies as high as the upper border of the notochord (Fig. 12, *Sy. G. 2.*), while in the preceding stage it was on a level with the lower border of it.
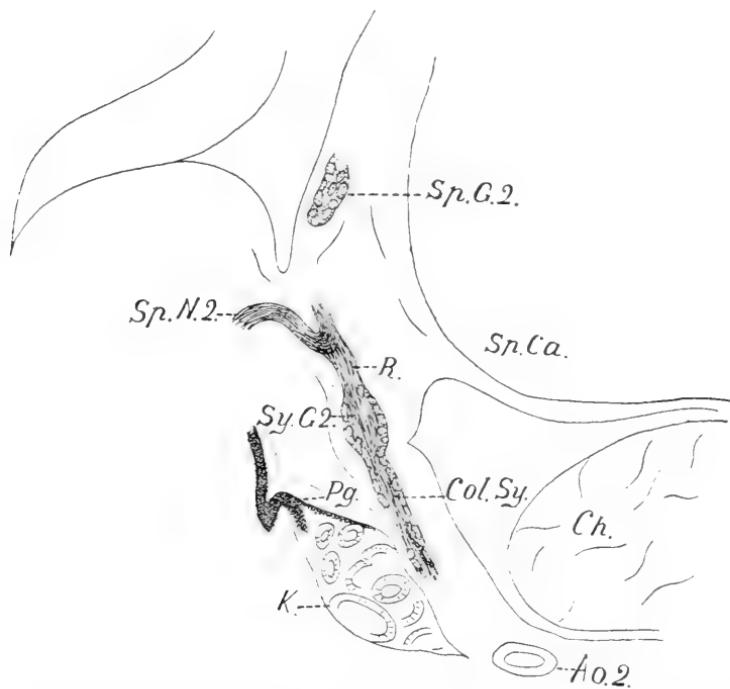
Fig. 12.—Transverse section through the second spinal nerve, from a toad in which the tail has almost completely disappeared. *Col. Sy.*, collateral sympathetic. *R.*, ramus. *Sp. G. 2.*, ganglion second spinal nerve. *Sp. N. 2.*, second spinal nerve. Other abbreviations, same as in preceding figures. For development of ramus, cf. Fig. 4. × 246. Camera lucida. Reichert, oc. 4, obj. 3.

The ridge and the structure with which it was connected, have now atrophied almost completely. Nearly all of the rami communicantes have become much longer, and the collateral sympathetic also is well developed (Fig. 12, *Col. Sy.*), while the differentiation of ganglia and commissures is now almost complete.

Summary.

(1)   In the region between the vagus ganglion and the second spinal nerve, the sympathetic arises in a comparatively simple and direct manner : cells, probably of epiblastic origin, scattered in the mesoblast gradually become aggregated (Fig. 2, *Sy.*) to form a cellular cord.   This is similar to the process in mammals described by PATERSON, except that he finds the cord is at first entirely independent of any other structure, while in the toad the cells of the sympathetic cord lie in contact with the fibers of the first and second spinal nerves, from the earliest stages.

(2)   In the region posterior to the second spinal nerve, the origin of the sympathetic system is more complex.   It appears first as a small ridge of cells (Fig. 1, *Ri.*) lying close along side the aorta.   The cells at the top of this ridge, as it becomes higher, are differentiated to form the sympathetic cord (Fig's. 5 and 6, *Ri.* and *Sy.*).   Later, the ridge disappears entirely, leaving the cord free, save its connections with the collateral sympathetic and with the spinal nerves (Fig. 12, *Col. Sy.* and *R.*).

(3)   The sympathetic ganglia and commissures arise directly from the sympathetic cord.   The latter becomes enlarged in the region of the nerves, forming the ganglia, while the portions between the nerves become reduced, forming commissures, which, immediately after metamorphosis, are composed largely of nerve fibers.   (Fig. 11 shows the enlargements and the constricted portions.)   These findings contrast somewhat with the observations of BALFOUR on elasmobranchs, where he finds that the ganglia arise entirely independent of each other, the commissures appearing later as outgrowths from the ganglia.

(4)   The rami communicantes arise in the toad in the same manner as in elasmobranchs (BALFOUR).   The cord (the ganglion in elasmobranchs) lies in contact with the nerve from the very first (Fig. 4, *Sy.*).   Later it gradually is removed from the nerve, retaining, however, fibrous connections, which constitute the ramus.   The rami appear earliest in the mid-trunk region, my preparations showing the first one in connection with the

sixth nerve . (12 mm. stage).   The first and the ninth are the last nerves to develop rami.

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EDITORIAL.

CONCERNING THE GENETIC RELATIONS OF TYPES OF ACTION.

Even a superficial and casual examination suffices to convince one that the commonly recognized varieties of activity—reflex, instinctive, voluntary, habitual. etc.,—are intergrading types, not sharply separated classes. Concerning the fact of the existence of clearly definable types of action there is no dispute ; concerning their genetic relations there is surprising lack of agreement. Some maintain, with SPENCER, that activity developes from the simple to the complex, from reflex action, through instinctive, to voluntary action. Others, especially those who have attended more carefully to the development of action in the human subject than in the animal kingdom generally, with equal assurance insist that the true and primary course of development is from the relatively complex, variable, and apparently voluntary act to the reflex, automatic and habitual. It is my purpose in this discussion of the subject to try to show that these two courses of development are supplementary rather than contradictory, that phylogeny presents us with facts which favor the former view, ontogeny with facts which favor the latter.

For present purposes it will suffice if we select as essentially important types of action the reflex, the instinctive, and the voluntary. An examination of typical acts to which we should unhesitatingly apply these terms indicates that the types may be defined in terms of the complexity and variableness of action. The reflex act is simple and uniform ; the instinctive act is more complex as well as more variable ; the voluntary act is either simple or complex and extremely variable—unique. These facts are conveniently expressed in the following simple classification :

Simple Acts $\left\{\begin{array}{l}\text{Uniform (Reflex, Automatic, Habitual)}\\\text{Variable (Instinctive)}\\\text{Unique (Voluntary)}\end{array}\right.$

Complex Acts $\left\{\begin{array}{l}\text{Uniform (Habitual, Automatic)}\\\text{Variable (Habitual)}\\\text{Unique (Voluntary)}\end{array}\right.$

Furthermore, it will be convenient for us to consider that single uniform response to a simple external or internal stimulus which is called a reflex as the unit of activity. Then, according to the degree of variableness, the same relatively simple act may be classed as reflex, instinctive, or voluntary. The frog when it responds to a touch near the nostril by raising its fore leg as if to brush away the stimulating object, for all that we can tell from a single reaction, may be reacting in any one of the three ways. Only by careful observation of a series of reactions to the same situation can that information which is necessary for the classification of the act be obtained. If with each repetition of the stimulus the same reaction occurs immediately and with no perceivable variations, we class it as a reflex. If the series presents acts which, although essentially the same, vary slightly from one another, so that only the general form of the reaction is predictable, we apply the term instinctive. And, finally, if from time to time new acts appear in the series, so that the reaction can never be predicted, the acts are voluntary. As a usual thing, however, instinctive and voluntary actions are more complex than reflexes, and analytic study reveals that they are really made up of a number of simple reflexes closely associated. It was the discovery of this that led LOEB[1] to speak of the instinctive act as a chain-reflex.

Possibly it is worth while to present an illustration of these types of action and their differences as exhibited by the frog. Suppose the conditions of reaction to be the following. To the stimulus of a touch on the nose the animal reacts by, 1) a leg movement, or 2) a head movement, or 3) locomotion, or 4) a combination of the three. Then, according to the degree of variableness of the reaction series, the reaction would be classed as:

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[1]Comparative Physiology of the Brain and Comparative Psychology, p. 178.

I. Reflex, if, for example, the reaction series
    read 1–1–1–1–1–1 or 2–2–2–2–2–2 or 3–3–3–
    3–3–3 etc.

II. Instinctive if the reaction series read 1, 2–1,
    2–1, **2**–1, 2 etc.   In this series of numerals
    differences in weight indicate slight variations
    in the emphasis of the various units of the ac-
    tion.

III. Voluntary if the reaction series read 1, 2, 3–
    2, 3–3–2–1, 3 etc.

Leaving difference in complexity out of consideration for
the moment, the reflex act is uniform, the instinctive variable,
the voluntary unique.

'Having now defined our reaction types, we may note that
comparative studies show that animals differ with respect to
their activities in two fundamentally important directions : first,
in the number and variety of the reactions which they are ca-
pable of giving in response to a particular stimulus-complex
(situation); and second, in the rapidity with which they are able
to narrow down the trial and error series of reactions to those
acts which are appropriate to the situation.   From one point of
view this is learning, from another it is the mechanizing of ac-
tivity.   The former of these differences may be known as the
scope of reaction; the latter, as ability to profit by experience.
Organisms in markedly differing degrees, according to their
complexity of form and environmental relations, follow the in-
junction ''prove all things ; hold fast that which is good.''

Of chief interest in this connection is the recently discovered
fact that even the simplest organisms are not exceptions
to this rule, for JENNINGS has noticed that Paramecium,
Vorticella, Stentor and many other unicellular forms exhibit
the trial and error method of reaction ; and more recently
HOLMES[1] has described the same type of reaction in the
earthworm and other invertebrates.   These discoveries prove
the falsity of the prevalent notion that simple organisms exhibit
single simple stereotyped reactions which are suitable in
the long run, but show no signs of adaptation or even of

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[1] The selection of Random Movements as a Factor in Phototaxis. This
Journal, **15**, 100.

such trial and error reactions as are common among more complex animals. It would appear rather that all animals more or less thoroughly prove or test their environment by the method of trial and error. Sometimes we find a wide range of reactions, as in the cat, dog and monkey ; and again we find a narrow range, as in the unicellular organisms. Organisms differ, then, not in the essential method of reacting, but, first, in the scope or variety of reactions exhibited in the proving of things, that is, in the thoroughness with which they are capable of testing a situation ; second, in the influence which the tests have upon subsequent reactions. According to JENNINGS and other students of simple forms of animal behavior, the unicellular organisms go through much the same series of trial and error reactions each successive time a situation is presented to them ; they do not in any marked degree profit by their experience. Higher organisms, on the contrary, give unmistakable evidence of profiting by their proving of things, for from the chance stumbling upon the right act which is characteristic of the trial and error method at first, they progress to the point at which the right reaction is given as soon as the situation is presented : they learn, by experience, the appropriate form of reaction. Some animals quickly lay hold upon that which is good and tenaciously hold to it, others profit scarcely at all by the repetition of a reaction. Certain animals continue to stumble upon the right reaction from the beginning to the end of life, others become able to select the profitable reaction. In general the statement is true that those organisms which most nearly prove all things are also best able to hold fast that which is good, but as will be shown later there are certain striking and significant exceptions to this rule.

If, now, we seek for the developmental relations of the two aspects of activity which have been selected as primarily significant—scope of the reaction series and ability to learn, with its resultant mechanization of action—we note that the scope of reaction is primarily a phylogenetic aspect, ability to learn an ontogenetic aspect. For in the race, generally speaking, activity develops from the simple uniform series of trial reactions to

the complex variable series ; there is change from generation to generation in the number and variety of reactions exhibited in the trial and error series. At times these changes are not in the direction of an increase in the scope of reaction, for in certain cases regress in one direction conditions progress in another : the developmental process is not simple and continuous. In the individual, on the other hand, repetition of a reaction brings about mechanization ; habits are formed ; the number and variety of reactions which were exhibited early in the life of the organism are diminished later by the avoidance of those which are useless or harmful Plasticity in activity is an aspect of phylogenetic development; fixity in activity, of ontogenetic development.

Precisely such a point of view with reference to aspects of activity as is here taken necessitates a justification of the separation of phylogeny and ontogeny. Why should we speak of one aspect of action as characteristic of phylogenetic development, another of ontogenetic ? The answer to this question is found in the history of activity. For if we choose a type of organism which is capable of associative learning we find that any individual of the species during its life exhibits two kinds of action: first, reflex, instinctive and voluntary acts which are not shaped by experience ; second, instinctive and voluntary acts which are modified by experience, and which in case of the latter give rise to habits. The first represents the hereditary ability of the individual ; the second, the acquired ability. In the offspring of the individual there appear hereditary activities similar to those of the parent, but not exactly like them, for no two individuals have precisely the same form. There are more or less marked variations, and for the development of activity these variations are of great importance. The reflexes of a species appear in generation after generation with but slight and usually unnoticed changes ; the instinctive acts show greater differences, the old ones are modified and new ones appear, possibly as the result of the inheritance of certain of the tendencies to action which have been established as habits in the parent ; the voluntary acts are strikingly different, unique. It is here that variation

brings about those changes which determine the course of the development of activity in the race, changes in the scope of reaction. The trial and error series may be longer in the offspring than in the parent; if so we speak of the animals greater scope of reaction and of its greater originality or initiative. The connecting link between ontogenetic and phylogenetic development has to be sought in the value of habits to the race. If the results of individual experience are transmitted, it is clear that a species may gain a larger fund of instincts while at the same time becoming capable of a wider range of reactions. Variations form the basis of changes in the scope of reaction; the inheritance of acquired tendencies to action accounts for changes in instinctive action. Each new generation may possess new instinctive acts, in addition to new possibilities of voluntary action.

But the animal kingdom presents, instead of uniform increase of plasticity and fixity (scope of reaction and mechanization) with increase in complexity of structure, divergent lines of development. Certain animals are markedly plastic or voluntary in their behavior, others are as markedly fixed or instinctive. In the primates plasticity has reached its highest known stage of development ; in the insects fixity has triumphed, instinctive action is predominant. The ant has apparently sacrificed adaptability to the development of ability to react quickly, accurately and uniformly in a certain way. Roughly, animals might be separated into two classes : those which are in high degree capable of immediate adaptation to their conditions, and those which are apparently automatic since they depend upon instinctive tendencies to action instead of upon rapid adaptation.

Attention to these and other striking differences in behavior should enable us to make a valuable classificatian of animals on the basis of activity. Certainly it is apparent, and it can not be better exhibited than by reference to such facts as those under consideration, that there has been no one direct course of development in animal behavior ; rather, there seem to be several directions of development, of which the present highest stage of one is marked by the insecta, that of another by the primates.   ROBERT M. YERKES.

THE BASIS FOR TAXIS AND CERTAIN OTHER TERMS IN THE BEHAVIOR OF INFUSORIA.

In the directed reactions of lower organisms we find repeated attempts by various authors to distinguish in one way or another two great classes of phenomena, and for these two classes different terms have been used. Thus ROTHERT[1] distinguishes two sorts of taxis, strophic and apobatic, depending on the manner in which they are brought about. Strophic taxis corresponds to the typical taxis or tropism of VERWORN or LOEB. It is conceived as brought about by a turning of the organism toward or from the source of stimulation, due to a difference in the intensity of action of the stimulus on the two sides or ends of the organism. Apobatic taxis is defined as produced by a backward movement at passing from one concentration to another.[2] The typical case for this is the reaction method of bacteria. ROTHERT includes under apobatic taxis the reaction of Paramecium and other infusoria to chemicals, etc., though for this his definition is inadequate, since the backward movement is only a comparatively unimportant detail of the behavior, and is often omitted.[3]

PFEFFER[4] rejects ROTHERT's terms, substituting for strophic taxis the word topotaxis, for apobatic taxis the word phobotaxis. MASSART[5] applies the term taxis only to the phenomenon called by ROTHERT strophic taxis, while the word phobism is proposed for the backward movement called by ROTHERT apobatic taxis.

DAVENPORT[6] makes in his discussion of the reactions to light a distinction corresponding to a certain extent with those already mentioned. He distinguishes reactions whose direction is determined by the direction of the rays of light, from re-

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[1] *Flora*, **88,** 1901, p. 393.
[2] *Rothert, l. c.* p. 393.
[3] See the account by the present author, this Journal, **14,** 1904, pp. 458-460.
[4] Pflanzenphysiologie, Bd. 2, 1904, p. 755.
[5] *Annales de l' Institute Pasteur*, 1901, p. 25.
[6] Experimental Morphology, vol. l, 1897, p. 180.

actions whose direction is determined by differences in intensity of illumination. The former he calls phototaxis, the latter photopathy. Photopathy is held to be due to the fact "that increased brightness causes a movement forwards, that a diminution of brightness causes a movement backwards, or *vice versa,* thus resulting in an accumulation of the organisms in the darker or lighter parts of the field." (l. c. p. 210.) Phototaxis on the other hand "includes that active migration of organisms whose direction is determined by that of the rays of light" (p. 180). In elongated organisms DAVENPORT thinks that phototaxis is due to the difference in intensity of illumination of the two sides of the organisms (p. 209), while in Amœba he thinks it possible that the direction taken by the ray in passing through the organisms is the determining factor (p. 210). YERKES[1] holds, with HOLT and LEE, that both phenomena are due in some way to the intensity of the light, and classes as taxis those reactions in which the direction of movement is determined by orientation, while -pathy includes reactions in which the movement "is not definitely directed through the orientation of the organism." This distinction doubtless indicates the real observational source of the attempt to separate two great classes of reactions, and does not attempt to make the definition outrun the known facts.

Kinesis is a term which seems to have been first used by ENGELMANN[2] for the increase or decrease of activity produced by certain agencies. The fact that certain bacteria increase or decrease movement in the light he called photokinesis. ROTHERT (*l. c.*, p. 374) accepted the term kinesis for such changes in the amount of activity produced by chemicals, calling this chemokinesis. LOEB[3] had observed similar phenomena and applied to them the German word *Unterschiedsempfindlichkeit.* GARREY,[4] working with LOEB, later substituted the term kinesis for the German word. The term *Unterschiedsempfindlichkeit,* signifying literally sensitiveness to differences, might well include much more than a mere increase or decrease of activity ; it could properly

[1] Mark Anniversary Volume, 1903, p. 361.
[2] *Arch. f. d. ges. Physiol.,* **30,** 1882.
[3] *Arch. f. d. ges. Physiol.,* **54,** 1893, p. 81.
[4] *Am. Journ. Physiol.,* **3,** 1900, p. 29.

embrace all reactions due to a change in the intensity of action of a stimulating agent. GARREY's use of the term kinesis seems a little uncertain, since he seems in one place (p. 292) inclined to consider it equivalent to DAVENPORT's -pathy, thus including directed reactions to changes in intensity, while in general he seems to limit it to increase or decrease of activity, in the sense in which it was employed by ENGELMANN and ROTHERT. GARREY uses the term in contradistinction to tropism, which is defined in accordance with the well known views of LOEB.

Terms ending in -metry have been contrasted with taxis, especially by STRASBURGER[1] and OLTMANNS,[2] to distinguish those features of the reactions that are determined by differences in the intensity of the stimulating agent. Photometry is employed by STRASBURGER to signify especially the phenomenon that some organisms move toward the source of light in a certain intensity of illumination, while they move away from it at a higher intensity. By OLTMANNS photometry is used of any reactions due to differences in the intensity of light; ''movements produced by light of different intensity could fittingly receive the name photometric movement'' (OLTMANNS, *l. c.*, p. 190).

Thus we find various attempts to distinguish by one criterion or another two great classes of reactions. On the one hand we have apobatic taxis (ROTHERT), phobotaxis (PFEFFER), phobism (MASSART), kinesis (ENGELMANN, GARRY and others), -pathy (DAVENPORT), -metry (STRASBURGER and OLTMANNS); in these orientation is not a marked feature. On the other hand we have tropism or taxis proper (LOEB, DAVENPORT, MASSART, VERWORN and others), strophic taxis (ROTHERT), topotaxis (PFEFFER); in these orientation is a marked feature. What is the precise basis for this distinction into two classes?

In the behavior of infusoria (ciliates and flagellates) it is possible to distinguish clearly the two classes of phenomena on which this distinction is based, and to determine the real nature of the difference.[3] In both classes the cause of reaction is, in

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[1]*Jena. Zeitschr. f. Naturw.*, **12.** 1878.   [2]*Flora*, **75,** 1892, p. 183.

[3]In the effects of the electric current the usual reaction method is in the Ciliata interfered with by the forced cathodic reversal of the cilia,—a factor not par-

the infusoria, some change in the relation of the organism to the environment. It is usually, or perhaps universally, a change in the intensity of action of a stimulating agent on the body as a whole or on its most sensitive portion. The organism, having been in one condition, passes to another, and it is the transition that acts as the effective stimulation. In one of the two classes of reactions to be distinguished, the effective stimulation is due to the fact that as the organism progresses from one region to another it meets different conditions, and to the changes thus caused it reacts. This is the case under natural conditions with the reactions to mechanical stimuli, to heat and cold, to chemicals, to osmotic pressure, and to light when passing to a region of greater or less intensity of illumination. The cause of reaction is analogous to that in our own case in passing from a region of moderate temperature to a hot or cold region. The differences determining reaction are here arranged along the axis of the course, so that it is the backward or forward movement that brings them into action. The reaction is a change of movement such as to carry the organism successively in many directions—a series of trial movements. As soon as one of these movements carries the organism away from the stimulating agent—that is, in such a direction that the changes to which it subjects the organism lead toward the optimum instead of away from it—the reaction ceases, since the cause for it has ceased. The organism therefore continues in that direction. The position of the body has little or no effect on the production of the change that causes stimulation, or on the release from stimulation. The organism might retreat from the stimulating agent backward or forward or sideways ; in the one case as in the other it would be relieved of the stimulating changes. The different individuals may swim away directly or obliquely, their

alleled under any other conditions. As a result of this interference the reaction of the ciliates to the electric current takes in many respects a different character from the rest of their behavior. I wish therefore to emphasize the fact that the general relations set forth in the text do not apply to the reactions of the ciliates to this agent. Save for the forced cathodic reversal of cilia the response to the electric current would fall in our second class of reactions, as it actually does in the flagellates and rotifers.

various paths crossing at all sorts of angles ; the only require-
ment is that the path shall on the whole lead away from the
greatest (or least) intensity of the stimulating agent. Hence
when many specimens react in this way their paths need
not be parallel, and as a rule no marked orientation results.
When a common orientation of many individuals does occur, it
is produced through "exclusion,"—through the fact that under
the given conditions movement in any direction but one causes
the changes which act as effective stimuli, so that all are forced
to move in that direction. The behavior of Oxytricha in react-
ing to heat, as shown in Fig. 7 of the author's paper on Reac-
tion to Heat and Cold[1] will serve as a type for this reaction
method. It is, so far as the infusoria are concerned, the basis
for apobatic taxis (ROTHERT), phobotaxis (PFEFFER), and -pathy
(DAVENPORT), and might farther be classed, from certain points
of view, as kinesis or -metry.

The second class of reactions includes those in which the
changes that act as stimuli are brought about by a swerving to-
ward one side or the other, while the movements in the axis of
progression have no such effect. In the infusoria movements
from side to side are of course a regular part of the locomotion.
In the reactions to the effects of water currents, of centrifugal
force, of gravity, and of light rays coming from one side, the
lateral movements of unoriented animals induce marked changes.
In a water current or under the action of a centrifugal force, or
of gravity, lateral movements meet with less resistance in one
direction, greater resistance in another direction, and these
changes of resistance act as stimuli. In light coming from one
side the sensitive anterior end is more illuminated as the organ-
ism swerves towards one side; less illuminated as it swerves to-
ward the other, and these changes act as stimuli. The reaction
is the same as in the first class ; the organism changes its course
by a series of trial movements. It continues these movements
till it comes into a position in which it is no longer subjected to
the changes that act as stimuli. Such a position is found only
when the axis of the course coincides with the direction of ac-

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[1]Carnegie Institution of Washington, Publication 16, 1904, p. 16.

tion of the impinging force ; in other word, when the organism is oriented. The anterior end will be directed toward the source of the stimulating agent or away from it, according as it is the decrease or increase in intensity that is the effective stimulus[1]. The transference of the organism along the axis of progress has in these cases no effect on the relation of the organism to the stimulating agent, so that so far as this reaction is concerned backward progression might take place as well as forward. Under these stimuli a certain orientation of the organism, not a certain direction of progress, is the essential result of the reaction. This class of reactions forms the basis, so far as the infusoria are concerned, for taxis proper (MASSART, DAVENPORT, etc.), strophic taxis (ROTHERT), and topotaxis (PFEFFER).

Thus in the first class of reactions the essential result is a certain direction of progression—toward a region of greater or of less intensity—while in the second class the essential result is the orientation. But in both classes the nature of the stimulus is the same and the reaction is the same. The stimulus is some change in the relation of the organism to the surrounding conditions—a change in the intensity of action of some agent. The response is a motor reaction that consists of a series of trial movements. The response continues in each case until the effective stimulus comes to an end, then the usual motion is resumed. In the first class this does not produce orientation (save sometimes by "exclusion"), because stimulation comes to an end without it. In the second class it does produce orientation, because stimulation does not come to an end without it. The difference between the two classes depends on the peculiar difference in the distribution of the stimulating agent, not upon different ways of reacting on the part of the organism. The reaction is by "trial" movements continued till a cessation of the effective stimulation is brought about ; this will lead to orientation or not, just as the conditions require.

H. S. JENNINGS.

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[1]For details as to this relation, see this *Journal*, **14**, 1904, pp. 470, 472, and 478 ; Carnegie Institution, Publication 16, 1904, p. 60.

THE PROBLEM OF INSTINCT.

In the whole field now awaiting the student of mental life in animals, there is nothing of more cardinal interest and importance, both for animal psychology in itself and for general psychology, than the group of problems centering about the development of the conative life.   And of these problems none promise results so significant in themselves or so generally illuminative of the mechanism of mind, as the problem of instinct.   The question of the origin of instincts ranks as a classic.   Many prominent naturalists and psychologists have taken a distinctly anti-evolutional view of the matter, claiming intelligence and volition as the source of instincts.   They make a good case; at least there are facts of introspection which point unmistakably in this direction.   On the other hand, the facts at our command point to an evolution of mental processes as well as of physical structure.   Instinct is clearly the conative life of lower forms.   They seem to have no other conative life.   Higher forms have both instinctive and intelligent conation.   But it is still an open question whether the instinct is the result of the automatization of volitional processes, or whether it is the unconscious reaction which has been selected by the environment and is thus the precursor which prepares the way for volition.

The adaptation to the environment, through complex and yet very fundamental instincts, as well as the fact of habit formation in the individual life, make for the view that *choice* is a factor in the formation of instinct.   On the other hand, the general order of evolution and development would place the simple, the instinct, before the more complicated volition.   Volitions may be comparatively simple and instincts may be quite complex.   But the general plan of the instinct marks it as an earlier form than the volition. We certainly have the indubitable evidence of introspection for this order in ontogenesis.   And we see the same order in the mental development of the child.   The same is true in the phylogenetic series; but the further we go from a ner-

vous system like our own, the greater becomes the merely anal-
ogical element, and the less trust we can place in the inference.

But indisputable factual evidence can be brought to bear
for the definite answering of this question of the origin of in-
stinct—as to whether instinct in its simplest lines originates
through the automatization of volitional acts or not. That is,
we can obtain definite data concerning the functional and genet-
ic relations of instinctive and volitional processes in animals
which have both. The method we propose is simply this:—
Take an animal with well defined but comparatively simple in-
stincts. Make a careful study of its instincts, both as they come
forward in the growing animal and as they function in the adult
animal. Then devise a set of experiments, for the express pur-
pose of testing the intelligence of the adult animal, its power
and capacity for dealing with new conditions. In this way it
will be quite definitely ascertained whether the present intelli-
gence is such as would have sufficed for the determination of
the behavior of the same animal which now constitutes its in-
stinct. For it is a reasonable and necessary assumption that if
instinct arose thus through the automatization of volitional acts,
the present intelligence of the animal should be equal to deal-
ing as efficiently with similarly complex situations. For the
function of automatization is not to do away with intelligence by
rendering it useless, but to make possible its further advance by
providing for the ready performance of that which has been
learned already. This is the way it does work in our own de-
velopment.

Of course great care and skill will be required in devising
the experimental means of this test and in carrying them out.
Such criticisms as those made by Professor MILLS (*Science*, N.S.,
191, 745.) of Dr. THORNDIKE in particular and of the ''labor-
ators,'' as he calls them, in general, must be kept carefully in
mind. We must assure ourselves in every possible way, as by
checks and counter-checks and all possible variations, that the
stimulus is acting upon the animal in the way that we think it
is, that it is really attending in animal fashion to the situation
as we are thinking the situation, and that it is really feeling the

impulses which we think it is feeling. In other words we must use every means to ascertain the mental factors of the situation before offering any interpretation of the meaning of the behavior, or using the observed behavior to strengthen any particular theory of psychic functional relations We cannot hope for absolute certainty of the processes in other minds by any known method, and the certainty is less the further we recede from ourselves. But the careful student of the habits of the animal in its natural condition, by exercising care to have the animal in as nearly natural conditions as the experimental necessities admit of, and by being careful to isolate the experimental conditions for the animal, will be able to interpret the movements and incipient movements in mental terms and thus have a close approximation to accuracy in grading the intelligence of the animal as shown in the particular situation. Accurate and detailed knowledge of the natural life of the animal, it cannot be insisted too strongly, is of the highest importance both for the proper planning of experiments and for the interpretation of the results.

If under these conditions it can be shown that an animal now has a grade of intelligence sufficiently high to serve as the guide in shaping any and all of the instinctive modes of behavior with which it is equipped, it has not been shown thereby, of course, that intelligence was the means of its development. The development of mind may have brought fourth this grade of intelligence at a later stage in the race history than that at which the instincts took their rise. In this case the results would be merely negative. If, though, it can be shown that a given animal has, as its mental equipment, an intelligence too low to deal with a situation as complex as that dealt with by the instinct, the inference is then clear that the instinct has come by some other way than by intelligence. For our major premise, as before, is that intelligence as a whole never retrogrades, but when released through automatization proceeds to greater complexity and higher organization through dealing with more complex situations. This case would presuppose a retrograding and would therefore be impossible. And so it was not con-

scious (I do not mean self-conscious) choice which determined originally the mode of reaction which is now instinctive.

This position being established, the way would then be open for the psychologist to construct and maintain a theory of the origin of volition and cognition as developing out of a system of organic behavior. This negative evidence, if it can be found, will contribute to a constructive theory of the systematic development of mind as a progress from the simpler and less organic to the higher and more organic. For intelligence is both of these as compared with instinct.

T. H. HAINES.

A REVIEW OF SOME RECENT LITERATURE ON THE CHEMISTRY OF THE CENTRAL NERVOUS SYSTEM.

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The last few years have witnessed a marvelous impetus and great evolution in our ideas of anatomical and chemical facts concerning the central nervous system. The cerebro-spinal fluid has also shared in this advance, partly as the result of independent study, but chiefly because of its intimate relation to the nerve structures. The literature on the subject is scattered through the various journals and reports, but outside of Thudichum's book on the chemical constitution of the brain of man and lower animals, and of Sicard's recent work on the cerebro-spinal fluid, there has been no serious attempt to summarize the recent publications on the chemistry of the nervous system, both in normal and pathological states. It seems opportune, therefore, to review the most available facts along these lines, and point out in what manner these may be utilized to stimulate further research. Of course, in the limits imposed by a review, only the most important papers can be abstracted. The work on neuro-chemistry has been pushed in several directions, of which the principal ones merit the following subdivisions :

1. More systematic attempts at classifying the various substances of the brain.

2. The isolation of nerve products by newer methods.

3. The further ultimate analysis of these products.

4. The chemistry of the finer structure of the nerve cells, including the micro-chemistry of various stains.

5. The autolysis of brain tissue.

6. Analysis of the brain and cord in various normal and pathological states.

7. The chemistry of the cerebro-spinal fluid, particularly as a medium for the various products of nerve degeneration.

8. The physiological action of various normal and pathological nerve products.

The substances so far isolated from the brain follow. The classification is merely a tentative one and must not be looked upon as

final. It is partly adopted from THUDICHUM and KOCH and partly the result of my own observations.

A. Water.
B. Proteids.
    1. A globulin coagulating at 47°—50° C.
    2. A globulin coagulating at 70° C.
    3. Neuroglobulin, coagulating at 45°—50° C. (According to HALLI-
        BURTON it is the coagulation of this substance in the nerve cells,
        which is the physico-chemical cause of death from hyperpyrexia).
    4. Neurostromin (in traces).
    5. Nucleo-proteid (LEVENE, HALLIBURTON, SCHKARIN).
    6. Neurokeratin (KÜHNE and CHITTENDEN).
    7. Albumoses and Peptones.
C. Extractives.
    1. The purin bases of the nucleo-proteids (Adenin, guanin, hypo-
        xanthin).
    2. Pyramidin bases (thymin and cytosin).
    3. Amido-acids (leucin and tyrosin).
    4. Urea (also a normal constituent of the cerebro-spinal fluid).
D. Carbohydrates.
    1. Inosite.
    2. An unknown carbohydrate which gives the furfurol reaction and is
        probably related to the pentoses.
    3. Galactose (a split-product of cerebrin).
    4. Dextrose (in the cerebro-spinal fluid)—CORIAT.
    5. Pyrocatechin (in the cerebro-spinal fluid?)—HALLBURTON.
    6. Glycogen (?),
E. Acids.
    1. Nucleic acid.
    2. Sarcolactic acid.
    3. Lactic acid (optically inactive ethylidene lactic acid. This is the
        result both of post-mortem decomposition and of long continued
        activity in the central nervous system, as in convulsive seizures.
        In both cases, the acid passes into the cerebro-spinal fluid).
    4. Glycerophosphoric acid (a decomposition product of lecithin).
    5. Formic acid.
    6. Acetic acid.
    7. Succinic acid.
    8. Stearic, oleic acid, palmitic acids (decomposition products of lecithin).
    9. Litho- and Butophosphoric acid (THUDICHUM).
F. In Pathological Conditions.
    1. Cholin (a decomposition product of lecithin—MOTT and HALLIBUR-
        TON, DONATH, WILSON, CORIAT).
    2. Neurin.
    3. Uric acid.
    4. Kreatin.
    5. Trimethylamin (a post-mortem product).

6. Neuridin.

G. Inorganic bodies. Sodum, potassium, ammonium, calcium and iron, present either as dissociated ions, or in organic combination. The radicles Cl, SO_4, PO_4, and CO_3 are also present as disociated ions or with the cations above mentioned.

H. Lecithins (Monophosphatids containing one nitrogen molecule in the proportion N:P=1:1). The various lecithins from eggs, barley, malt, yeast and brain show variations in the amounts of phosphorus and in the methyl content.

    1. Lecithins (Stearylolely, margeryloleyl, palmityloleyl).

    2. Amido-lecithins (amido-myelin). Contains two nitrogen molecules N:P=2:1.

    3. Kephalins (P:N=1:1).
        Kephalin
        Oxykephalin
        Peroxykephalin
        Myelin
        Paramyelin
        Sphingomyelin
        Assurin (N:P:=2:2).

    4. Amido—Kephalins (amido-kephalin P:N=1:2).

I. Cerebrins.

    1. Phrenosin
    2. Kerasin (THUDICHUM)
    3. Amidocerebrinic acid—glycosid (BETHE)
    4. Phrenin
    5. Cerebrin acid
        Cerebrin acids
        Sphaerocerebrin
        Cerebrin phosphoric acid (BETHE)

J. Cholesterin (occurs both free and in the form of an ester).

K. Sulphur compounds (Cerebusulphatides and sulphatids of THUDICHUM).

L. Amido-fats (Krinosin and Bregenin).

As a contrast, THUDICHUM's classification alone should be consulted (Die chemische Konstitution des Gehirns des Menschen und der Tiere, pp. 89-91), and the reader will also find there a minute discussion of these various products, with particular relation to their chemical reactions.

It is unnecessary to enter here into the details of the newer methods for the isolation of the various brain substances. The original papers must be consulted, of which reference is given in the bibliography affixed to this review. It suffices to mention THUDICHUM's complete isolation methods, the acetone method of KOCH for the separation of lecithin, kephalin and cerebrin, LEVENE's methods for the isolation of nucleic acid and the nucleo proteids, KOCH's modification

of the method of HERZIG and MEYER for the quantitative determination of lecithin by an estimation of the methyl groups, HALLIBURTON's method for the detection of cholin in the cerebro-spinal fluid and blood, and CORIAT's method for the detection and quantitative estimation of cholin in nerve tissue.

The first serious attempt at the quantitative analysis of the brain in normal and diseased individuals, was that of GUTINKOV, who estimated water, fixed substances, nitrogen, sulphur and phosphorus, both in the white and grey matter. His series comprised 15 human foetal brains at about the third month, the brains of seven people who died suddenly without any previous illness, and of various mental and somatic diseases. These latter included three cases each of carcinoma and syphilis, two each of pulmonary tuberculosis, neurasthenia and senile dementia, four cases of acute alcohol poisoning, seven of chronic alcoholism, and one case each of post-epileptic dementia, idiocy, post-maniacal dementia, general paralysis, epilepsy, syphilitic pseudo-paralysis, mania and stuporous melancholia. A summary of his various findings as compared with the averages for normal brains, is readily seen from the following table. For the normal human brain, as the average of seven analyses, the following figures are obtained, and it is with these that the pathological material is compared.

Water (gray matter)	84.62	
Water (white matter)	69.73	
Phosphorus (gray matter)	1.2128 (dry)	0.1877 (moist)
Phosphorus (white matter)	1.378 (dry)	0.3454 (moist)
Nitrogen (gray matter)	8.9082 (dry)	1.3692 (moist)
Nitrogen (white matter)	5.5808 (dry)	1.6027 (moist)
Sulphur (gray matter)	0.6821 (dry)	0.0927 (moist)
Sulphur (white matter)	0.5250 (dry)	0.1589 (moist)

Disease.	Water in gray sub.	Water in white sub.	Phosphorus in gray sub.	Phosphorus in white sub.	Nitrogen in gray sub.	Nitrogen in white sub.	Sulphur in gray sub.	Sulphur in white sub.
Carcinoma	N	N	+	+	—	—	—	N
Tuberculosis	—	N	+	+	+	N	+	N
Syphilis	+	+	+	—	—	+	—	—
Acute alcoholic poisoning	+	—	—	+	—	—	—	—
Chronic alcoholism	+	—	—	+	—	+	.	—
Post-epileptic dementia	+	+	—	—	+	+	—	—
Idiocy	N	N	+	+	+	+	+	+
Neurasthenia	—	—	—	—	+	+	+	+
Post-maniacal dementia	+	+	—	—	—	+	+	+
Neurasthenia	+	—	—	—	—	—	—	+
General paralysis	+	+	—	—	+	+	+	—
Senile dementia	+	+	—	—	—	—	—	+
Epilepsy	—	—	+	+	+	+	+	+
Syphilitic pseudo-paralysis	+	+	—	—	+	+	—	+
Mania tranquilla	—	—	+	+	+	+	—	—
Melancholia	—	+	+	—	—	+	+	—
Senile dementia	+	—	—	—	—	+	+	+

(N = normal. + = increased. — = decreased).

The figures themselves, for which the original article must be consulted, are certainly far from convincing, the pathological material especially showing some glaring contraditions; for instance, the difference in the two analyses of neurasthenia and senile dementia. Furthermore, the figures on the percentage of water in general paralysis, are not as high as the marked pial oedema of this disease would lead us to believe.

THUDICHUM's figures are the result of the working over of a large amount of material and of complex elaborated methods. For the gray matter of the human brain he gives the following results :

Substance.	*Percent.*
Water	85.270
Neuroplastin	7.608
Ether extract (with kephalin, lecithin and cholesterin)	1.950
Cerebrosides, cerebrinic acid and myelin	0.424
Lecithin, kephalin and myelin (out of the last oily material)	0.780
Inosite	0.193
Lactic acid	0.102
Alkaloids	--------
Sulphuric acid and neuroplastin	0.06
Sulphuric acid in extract	not estimated
Phosphoric acid	0.017
Potassium	0.025
Sodium	0.092
Watery extract	0.500

For the white matter of human brain :

Substance.	*Percent.*
Water	70.230
Neuroplastin	8.630
Ether extract (kephalin, lecithin and cholesterin)	11.497
Cerebroside and myelin	6.910
Lactic acid	0.0456
Inosite	0.2171
Alkalies (as carbonates)	0.1717

The following figures were established for the entire human brain, as the sum of results from separate analyses of the two hemispheres, cerebellum, mid-brain and medulla, gray and white matter. The figures are given in grammes, and relate to the entire weight of the brain without membranes (1296 grammes).

Neuroplastin	101.20
White matter	55.46
White matter (insoluble in ether)	33.57
White matter (soluble in ether)	21.84
Buttery material	56.76
Kephalin	5.94
Myelin	15.30
Lecithin	11.75
Cholesterin	24 21
Inosite	1.94
Lactic acid	2.14
Hypoxanthin	3.35
Extractives	9.00
Potassium	0.78
Sodium	1.06

KOCH's figures were obtained from the brain of an epileptic. The analysis was conducted with great care and with the aid of more recent and accurate methods.

Substance.	Corpus callosum.	Cortex (prefrontal)
Water	67.97	84.15
Simple proteids	3.2	5.0
Nucleo-proteid	3.7	3.0
Neurokeratin	2.7	0.4
Extractives	1.51	1.58
Inorganic salts	0.82	0.87
Lecithins	5.19	3.14
Kephalin and myelin	3.49	0.74
Amido-lecithins	Trace	Trace
Phrenosin and Kerasin	4.57	1.55
Cerebrin acids	Trace	None
Cholesterin	4.86	0.7
Sulphur compounds	1.40	1.45

The wide differences in the figures of these two investigators show how far we are from establishing a comple quantitative composition for the normal human brain. Such figures can only be obtained as the average of a large number of analyses, and they must be firmly established and fully available before we can hope to make any comparison with pathological brain material.

The recent studies that have been made on pathological brains and cords, have related mainly to diseases where there is extensive general or focal destruction of nerve tissue, as in general paralysis and hemiplegia, comparisons with microscopical findings being made at the same time. W. BARRETT, as the result of the analyses of the brains and cords in general paralysis, found an invariable increase in

the water, while phosphorus was always slightly decreased, but this decrease seemed to bear no relation to the extent of fiber degeneration or cell chromatolysis. NOLL, in an experimentally degenerated sciatic nerve, found a decrease of phosphorus and of the alcoholic extract. CORIAT found cholin in the peripheral nerves, brain and cord of a case of alcoholic polyneuritis, the amounts being parallel to the extent of the MARCHI reaction. The presence of the alkaloid here must be looked upon as the result of autolytic processes in the lecithin.

MOTT and BARRETT, as the result of analysis of two cords from cases of hemiplegia, concluded, (1) that on the degenerated side of the cord a breaking up of the phosphorized fat occurs, (2) the amount of lecithin present is diminished, (3) fat is present in excess, (4) the amount of extractives soluble in ether is increased, (5) the proteid residue is diminished, (6) the phosphorus is diminished, (7) the ether extract has a buttery appearance instead of being crystalline. HALLI-BURTON has shown that the cause of death from hyperpyrexia is a physico-chemical one, being due to the coagulation of the cell-globulin, and when this constituent of cell protoplasm is coagulated, the protoplasm as such is destroyed. The temperature for this reaction is 47° C, but temperatures as low as 42° C will have the same effect if continued sufficiently long.

So far there have been published only two studies on the important question of the autolysis of brain tissue, those of LEVENE and CORIAT. The former established the presence of an intracellular proteolytic enzyme in fresh brain tissue, and which acted only in an acid medium. CORIAT, working from the standpoint of the genesis of cholin in the central nervous system, on account of its importance as a toxic agent in producing the convulsive seizures of epilepsy and general paralysis, concluded that there exists in the brain an enzyme capable of splitting lecithin into glycero-phosphoric acid, stearic acid and cholin, the latter being detected and quantitated by means of its platinum compound. This enzyme acted only in neutral and slightly alkaline media, and like all enzymes it could be destroyed by heat.

HATAI, in studying the effects of starvation on the brains of white rats, found that the absolute weight in his starved groups was diminished, and there was an actual diminution of the water and an increase in the relative amount of extractives, from which he infers that the protein substance must have been mostly affected. It was therefore expected that changes in the cell bodies would be found, but no marked alteration of the NISSL bodies could be demonstrated. The same writer, as the result of injection and feeding experiments with

lecithin on white rats, to show its effect upon their growth, concludes as follows: White rats which received the lecithin either by injection or feeding, gained in body weight more rapidly than those which did not receive it, the gain in the experimented rats being on the average 60 % greater than in the controls. The relative weight of the central nervous system in the lecithin rats was normal and contained the same proportion of water and solids as in the controls, this being another indication of the normal character of the growth. The peripheral nerves in both groups also grew normally, as shown by the relative area of the axis cylinder to its sheath. The action of the lecithin appeared to be that of a stimulating agent for normal growth, and the rats which received it showed a greater power of resistance to unfavorable changes in their surroundings.

KOCH's work on the action of electrolytes on colloidal solutions of kephalin and lecithin is also of interest, as showing the possibilities of the study of metallic poisons on the various constituents of the central nervous system, from the standpoint of physical chemistry. These colloidal solutions, which form perhaps the nearest artificial approach to the substratum of the living cell, are precipitated by divalent kations, while precipitation is prevented by univalent and trivalent ones.

The most important constituent of the individual cell is the NISSL bodies, which consist principally of nucleic acid. This acid is not found pure, but in combination with proteids forming nucleo-proteids which are probably the most complex bodies in a living organism. These compounds have the property of acids, contain phosphorus and iron and also the purin and pyrimidin bases. There is also a carbohydrate, the exact nature of which is unknown, but which gives the furfurol reaction and probably belongs to the pentose group. The purin bases of cerebronucleo-proteid are adenin and guanin, and the pyrimidin bases, according to LEVENE, thymin and cytosin. The amount of phosphorus is lower than in the nucleo-proteids from other tissues. Under pathological conditions, especially in general paralysis, this nucleo-proteid passes into the cerebro-spinal fluid; the proteid in the normal fluid consists almost entirely of serum-globulin, nucleo-proteid being completely absent.

During the last few years the cerebro-spinal fluid has called forth an immense literature, partly because it may contain the products of nerve degeneration (cholin, glycerophosphoric and lactic acids, lecithin?), and partly because in conditions of acute or chronic inflammatory processes in the brain, certain cells may appear in the fluid, the finding of which is a valuable diagnostic aid. The chromo- and cyto-diagno-

sis of the fluid do not concern us here. The chemistry of the fluid will be touched upon, only so far as it relates to the products of mye-lin decay. The physical chemistry of the fluid (freezing point, etc.), the various proteids and the reducing body are all of interest, but their consideration would exceed the scope of this review.

The most important chemical substance which passes into the cer-ebrospinal fluid is cholin, which is the nitrogen-containing methyl group of lecithin, and can be looked upon as one of its autolytic de-composition products. In the normal fluid it is found in mere traces, but in the fluid from cases of general paralysis, as first shown by MOTT and HALLIBURTON, large amounts are present. Since HALLIBURTON first demonstrated cholin in general paralysis, in his Croonian lectures on the chemical side of nervous activity, it has been found in a multi-tude of other pathological conditions, but principally where recent and active nerve degeneration is taking place. The lecithin of the myelin sheaths of nerves, is decomposed, probably through the agency of some enzyme, into glycerophosphoric acid, stearic acid, and cholin. This latter is found in the blood and cerebro-spinal fluid, while it is ab-sent from the urine, except in experiments on animals, where the alka-loid is given subcutaneously or intracerebrally. When cholin appears in the fluid, there is also an increase of phosphoric acid therein (DON-ATH), this being another proof of its derivation from lecithin. In long continued activity of the central nervous system, as in convulsive seizures, lactic acid in large quantities appears in the cerebro-spinal fluid.

Cholin is detected by means of its platinum combination, with which it forms a double salt, and crystallizes in single large yellow octahedral and occasionally twin crystals, and easily differentiated from the plati-num salts of neurin and potassium, by reason of its solubility, percent-age of platinum and large size and grouping of the crystals. Since HALLIBURTON first pointed out its occurrence in general paralysis, the work has been further elaborated by MOTT, WILSON, DONATH and CORIAT. As a result it is found in many pathological states, where there is an axonal reaction with corresponding fiber degeneration (cen-tral neuritis), general paralysis, brain tumor, tabes, HUNTINGTON's chorea, delirium tremens, polyneuritis, epilepsy, senile dementia (es-pecially where there is great wasting of the cortex), cerebral hemor-rhage, beri-beri, POTT's disease, disseminated sclerosis, amyotrophic lat-eral sclerosis, focal myelitis, organic dementia, brain syphilis, chronic hydrocephalus (?) spina-bifida, neurasthenia (?) and hystero-epilepsy. It has also been found in the blood of animals after experimental sec-

tion of the sciatic nerve, and in the peripheral nerves, brain and cord in polyneuritis and in all these latter, the amount present was parallel with the extent of the MARCHI reaction. This is easily explained if we remember that the MARCHI reaction depends on the preciptation of metallic osmium by stearic and oleic acids which are decomposition products of lecithin. The action of cholin on blood pressure has been carefully studied by MOTT and HALLIBURTON, while DONATH has shown that the injection or intracerebral application of cholin produces in animals, strong convulsive phenomena, and he concludes from these experiments that the seizures in general paralysis and epilepsy are due to intoxication by this alkaloid.

In closing, we should like to say a few words on DONATH's latest, and in many respects, his most pretentious paper, on the significance of cholin in epilepsy. He examined for cholin in sixty-four cases, detecting it by means of the platinum compound. In addition to the organic cases, where its presence would be expected, he finds it in those which we look upon as being functional in nature (neurasthenia). In addition, he finds the myelin forms of lecithin in two of his cases. This seems to us extremely doubtful and altogether inexplicable. Although using the platinum compound as a means of detecting cholin, yet according to the drawings and photomicrographs appended to his paper, he does not confine himself to octahedral or hexagonal crystals for a positive reaction, but labels anything and everything of crystalline nature as "cholin," while we have always hesitated, and then put down as negative, what DONATH in a large number of cases calls a positive cholin finding.

The bibliography appended makes no claim to completeness; it merely gives those papers directly mentioned in this review, or those which have been consulted for the discussion of the material.

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Dégénération Nerveuse. *Rev. Neurologique*, April 30, 1904.

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Burkholder, J. F. The Anatomy of the Brain. A Study of the Human Brain from the Brain of the Sheep. A Manual for Students in Medicine, Biology and Psychology. With an introduction by Professor HENRY H. DONALDSON. 175 Pages, 32 Full Page Plates. Chicago : G. P. Engelhard & Co., 1904.

This is a laboratory manual designed to meet the needs of those for whom human material is not accessible in sufficient amount for thorough demonstration purposes. It is well adapted to serve this purpose in medical schools and colleges, the text being clear, the figures good and the arrangement logical. There are unfortunately several misprints, some of serious nature, such as the confusion in the designations of Plates VIII and IX. Plate IX is defective also in that it does not show as clearly as such a dissection should show the ventricular boundaries. On the whole, however, the work is very well done and the book deserves a wide circulation. It should do much toward moderizing the instruction on the nervous system, both in medical schools and colleges.　　　　　　　　　C. J. H.

Smith, G. Elliot. Studies in the Morphology of the Human Brain with special Reference to that of the Egyptians. No. 1. The Occipital Region. Records of the Egyptian Gov't. School of Medicine, Vol. 2, pp. 125-170, 2 plates and 47 text-figures. *Cairo*, 1904.

The ultimate purpose of this series of studies the author states to be anthropological. And he adds, "The aim of these preliminary morphological studies is to enable us to discriminate between important and valueless features, between the kind of information that is worth collecting and that which it would be a mere waste of time to seek." This, then, is the motive underlying the present elaborate comparative study of the occipital region : " to learn the relative value of the data upon which our conclusions are to be based." In reaching his conclusions regarding the homologies in this region (for which the original memoir must be consulted) the author studied more than 600 hemispheres of various Primates of every genus and about 2000 human hemispheres. The importance of the paper, however, lies not so much in the fixing of particular homologies as in the sifting out of the essential landmarks from the unimportant variations.　　　C. J. H.

Sterzi, G. Die Blutgefässe des Rückenmarks. Untersuchungen über ihre vergleichende Anatomie und Entwickelungsgeschichte. *Anatom. Hefte* (*Merkel u. Bonnet*), I Abt., **24**, 1904, pp. 364, 4 plates and 37 text-figures. This is an important contribution to a field which has been but little cultivated—the comparative anatomy of the blood supply of the spinal cord. The work is divided into two parts, anatomical and embryological. In the first, representative types of the several animal classes are successively described and in the second the development of typical species is followed. Each section is followed by a summary and a brief general review closes each part. The general conclusions are that the blood vessels of the spinal cord divide in such a manner as to bring about more effective nutrition of the nervous matter the higher we ascend in the animal series, and that the ontogenetic stages traced out represent stages in the phylogenies of their species.

<div align="right">C. J. H.</div>

Prince, Morton. The Course of the Sensory Fibers in the Spinal Cord and Some Points in Spinal Localization Based on a Case of Section of the Cord. *Journ. Nerv. Ment. Dis.*, **32**, 81-100. A stab wound in the neck severed both dorsal funicles completely and the lateral funicles on one side more deeply than on the other. Tactile sensation was preserved on one side, showing clearly that such sensation is not transmitted exclusively by the dorsal funicles. A study of the hemianaesthesia shows that tactile sensation is transmitted by the lateral funicles of the opposite side. The case is important as presenting an unusually clearly defined lesion with excellent opportunities for careful study. The paper is accompanied by a digest of the literature.

<div align="right">C. J H.</div>

Cushing, Harvey. The Sensory Distribution of the Fifth Cranial Nerve. *Bull. Johns Hopkins Hospital*, **15**, 213-232, 1904. An exhaustive and fully illustrated study based chiefly on clinical examination of patients previously operated upon for complete extirpation of the Gasserian ganglion and of the cervical nerves. The cutaneous distribution is mapped more accurately than has hitherto been done and also the mucous membrane field within the mouth. In the latter field the observations show complete anaesthesia to all forms of sensation, including such irritants as ammonia fumes, on the whole of the operated side, with two exceptions. (1) The area at the base of the tongue supplied by the glossopharyngeus retains not only its sense of taste, but also general sensation unimpaired. (2) The second exception is the preservation of sensation in the field supplied by the chorda tympani of the facialis. The sensation of taste is not affected

in the slightest degree in any of these cases, and, while ordinary tactile, thermal and pain sensations are abolished, there remains in this second field a sensibility to a moving contact which leads the author to suspect the existence of fibers of general sensation in the chorda tympani. This peculiar sensation was found to be totally absent, as well as gustatory sensation, in a case in which the operation had involved the facial as well as the trigeminus nerve.

The clinical data are controlled by a discussion of the adult anatomy, the comparative anatomy and the embryological relations, the results of which clear up several vexed questions of peripheral nerve distribution, as well as strengthen to the point of demonstration some of the homologies proposed by recent students of nerve components in the lowliest vertebrates.   C. J. H.

Pinkus, Felix. Ueber ein dem menschlichen Haar benachbartes Sinnesorgan. *Verhl. Ges. Deutscher Naturf. u. Aerzte.* 75 Versam., Cassel. Zweiter Teil II, Hefte, Med. Abt., pp. 344-346, 1904.

Dr. Pinkus describes the hair and its accessory structures and considers that in position and structure these parts are analogous to the scales of reptiles. The human hair preserves the triple-hair structure characteristic of all mammals though the schema is often reduced to a single hair. A rudimentary scale lies immediately in front of the hair, while the sensory organ under consideration occupies a position behind (i. e. in the acute angle of) the hair. Histologically this knob-like body consists of a broad cutico-papilla with thickened epidermis. This structure, the under surface of whose epithelium is composed of pallisade-like cells, is highly innervated. The theoretical conclusions, which seem perhaps considerably to overbalance the meagre descriptive portions, are as follows : "We have to do, therefore, with an organ of great antiquity the fundamental form of which is perhaps preserved to us in the form of a genuine epithelial sensory ridge, in *Hatteria punctata* presumably the oldest reptile.' Our author agrees with Keibel that the hair is "homologous with a specially modified part of a scale."   C. L. H.

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The author finds no cerebral fissures in the human embryo of 3¼ to 4 months. The so-called Fissura prima (vordere Bogenfurche of His) is not a true fissure, but it might properly be called a "sulcus olfactorius" or "fovea olfactoria." Contrary to the idea of His, also,

the corpus callosum, beginning in the lamina terminalis, expands into its adult relations by intussusception of new fibers, and not by actual coalescence of the hemisphere walls.   G. E. C.

Lewis, Warren Hermon. Experimental Studies on the Development of the Eye in Amphibia. I. On the Origin of the Lens. *The American Journal of Anatomy*, **3**, 505-536, 1904.

In this communication LEWIS reports a series of experiments upon the embryos of *Rana palustris* and *R. sylvatica*, in which the optic cup was severed from the brain and removed from its normal position before any fundament of the lens had appeared. The author interprets his experiments as proving that contact between the optic cup and the skin is necessary for formation of the lens, and that the power to take part in lens-formation is not restricted to any particular region of the skin or optic cup. These facts, he believes, are "entirely in opposition to WEISMANN's theory of determinants."   G. E. C.

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The chief cause of the rolling in of the cortex in the Ammonshorn is the atrophy of the medial wall of the hemisphere in the region of the plexus chorideus.   J. B. J.

Scaffidi, Vittorio. Ueber den feineren Bau und die Funktion der Hypophysis des menschen. *Arch. f. mik. Anat.*, **64**, Heft 2, 235-255, 1 Pl., 1904.

Two kinds of cells are present, distinguished by their staining properties, each of which probably produces a definite substance which helps to form the secretion of the gland.   J. B. J.

Kamon, K. Ueber die "Geruchsknospen." *Arch. f. mik. Anat.*, **64**, Heft 4, 653-664, 1 pl., 1904.

Esox, Trigla and calf. Sublimate *et al.*; iron haematoxylin; Golgi and methylene blue; maceration with 0.05% chromic acid. Figures from haematoxylin sections support the conclusion, "Es giebt weder in der Ceruchschleimhaut der Fische noch der Säuger Bildungen, mit den Geschmacksknospen verglichen werden können."

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Heath, Harold. The Nervous System and Subradular Organ in two Genera of Solenogastres. *Zool. Jahrb., Abth. f. Anat. u. Ontog.*, **10**, Heft 3, 399-408, 1 pl., 1904.

General description of the nervous system.   J. B. J.

Rubaschkin, W. Studien über Neuroglia. *Arch. f. mik. Anat.*, **64**, Heft 4, 575-626, 4 pls., 1904.

Cat. Staining with methyl violet after special method of fixation. Description of types of glia elements with classification accord-

ing to their genetic relations: glia-genetic cells, astrocytes of young form, astrocytes of definitive form, cells without processes. Relation of neuroglia to the vessels, to the nerve cells and fibers. Structure and relations of the ependyma. Many of the figures show lack of care and exactness, and some are inadequate to their purpose.

J. B. J.

Pinkus, F. Ueber Hautsinnesorgane neben den menschlichen Haar (Haar scheiben) und ihre vergleichend-anatomische Bedeutung. *Arch. f. mik. Anat.*, **65**, Heft 1, 121-179, 4 pls., 1904.

Man, ape, monotremes, reptiles. Histological methods and intra-vitam methylene blue. Deals with the homology of the organ in man with the Tastfleck in reptiles and of the hair with an undifferentiated part of the reptilian scale.

J. B. J.

Ballowitz, E. Die Riechzellen des Flussneunauges (Petromyzon fluviatilis L.) *Arch. f. mik. Anat.*, **65,** Heft 1, 68-85, 1 pl., 1904.

Ewing, Henry Z. The Functions of the Nervous System, with Special Regard to Respiration, in Acrididae. *Kansas Univ. Sci. Bull.*, **2**, 305-319, 1904.

The main object of Mr. EWING's investigations on several species of grasshoppers has been the study of the nervous control of respiration. In addition he has made a considerable number of observations on other functions of the nervous system. His results in the main corroborate those of BETHE, and point to the segmental character of many of the reactions of the insect.

The conclusions reached are based on effects observed after the removal of the various ganglia. While the supraoesophageal and suboesophageal ganglia are found to exercise no control over respiratory movements, each ganglion of the thoracic and abdominal ventral nerve cord appears to act as the center for the respiratory and general reflex movements of the segment in which it lies. Neither the supraoesophageal nor suboesophageal ganglion is the center for coördinated movements. These can be carried out by the insect after the entire head has been cut off. Removal of the supraoesophageal ganglion destroys the animal's power to inhibit reflexes, and it no longer executes swallowing movements. There is also a loss of tonus of the muscles and general weakness. The suboesophageal ganglion appears to have some control over equilibration.

F. W. C.

Lukas, Franz. Psychologie der niedersten Tiere. Eine Untersuchung über die ersten Spuren psychischen Lebens im Tierreiche. *Braumüller, Wein und Leipzig,* 1905, VIII + 276.

This book, although complete in a certain sense in itself, is issued as the first part of a general animal psychology which the author tells

us in his preface he may sometime finish. The present volume is con-
cerned with the Protozoa, the Coelenterata, the Echinodermata and
the Vermes.

After an excellent discussion of criteria of the psychic and an ex-
amination of various forms of activity in an introductory chapter on
the problems and methods of animal psychology, the author proceeds
to consider the materials for a psychology of the above named phyla
in accordance with the following plan:

A. Description of anatomy, especially of the nervous system.
B. Description of activities.
    I. Changes of substance: 1. Taking food, 2. Assimilation and
        dissimilation, 3. Excretion.
    II. Changes of form: 1. Adaptation and transmission, 2. Growth
        and reproduction.
    III. Changes of energy: 1. Apparent spontaneous manifestations of
        energy-change, movement, light, electricity, 2. Action of me-
        chanical, photic, chemical, thermic, electric and acoustic stimuli.
C. Consideration of the question of the existence of consciousness.
    I. Bearing of anatomical conditions, especially of the nervous sys-
        tem.
    II. Bearing of activities, especially of movements.
    III. Bearing of the question of the value of consciousness for the or-
        ganism.

As this outline indicates, the author follows in general the
scheme of classification of organic processes offered by VERWORN.
He gives brief, clear, structural descriptions, and satisfactory accounts
of well chosen typical modes of behavior. The work is not thorough
and exhaustive in its reviews of the literature of its topics, since it is
intended for the general biologist rather than for the specialist in ani-
mal behavior or comparative psychology.

So far as materials are concerned it presents nothing new, for the
author has taken all his structural facts directly from the works of
other authors, and the only original work he claims within the field of
activity is the verification of the reports of other investigators. Con-
sequently the only portion of the book of much value to the specialist
in animal psychology is that which is concerned with the author's con-
clusions, on the basis of the facts collected, concerning the existence
of consciousness in the animals of the phyla mentioned, and its values.

In brief, the conclusions stated are that the Protozoa give no
evidence of consciousness, that certain of the Coelenterata, the Hy-
roids, exhibit the first signs of consciousness in the animal kingdom,
while the Echinodermata and Vermes give evidences of somewhat
more complex forms of consciousness. The author is guarded in his

statements and places his conclusions upon clearly defined bases of inference, which he discusses at length in his introductory and concluding chapters.

This book is a valuable contribution to the text-book and student literature of animal psychology. R. M. Y.

Parker, G. H. Hearing and Allied Senses in Fishes. *Bull. U. S. Fish Commission*, 45-62, for 1902 (published in 1904).

Professor PARKER after an admirably clear and concise historical sketch of his subject describes a series of experiments in which by nerve cutting he succeeded in demonstrating the specific functions of the ear and lateral line organs of Fundulus, mackerel and menhaden.

Detailed work was done with *Fundulus heteroclitus*. According to the author this animal when normal responds to vibrations transmitted to the water of the aquarium by a tuning fork of 128 V. by movements of the pectoral fins and increased respiratory rate. After the eighth nerve has been cut these responses no longer appear, hence the author concludes that the fish possesses a sense of hearing.

Similarly it is shown that the reactions to slight mass movements of the water, which are characteristic of the normal Fundulus, are not given by individuals in which the nerves to the lateral line organs have been cut.

This work is of special interest and importance, first, because the experiments were simple in plan, carefully executed, and definite in their results; second, because the results themselves are in large part contradictory of much that has heretofore been published on the subject.

It is PARKER's belief that the cutaneous organs, the lateral line organs and the ear form a series of sensory organs which respond to mechanical stimuli of various degrees of delicacy. Gross stimuli perhaps effect the cutaneous organs chiefly, less violent stimuli act primarily upon the lateral line organs, and the most delicate mechanical stimuli affect the ear. R. M. Y.

Jennings, Herbert S. Contributions to the Study of the Behavior of Lower Organisms. *Carnegie Institution of Washington*, 1904, Publication No. 16, pp. 256.

First Paper. REACTIONS TO HEAT AND COLD IN THE CILIATE INFUSORIA.

As Paramecium swims it draws towards its anterior end a vortex of water which passes in a slender stream along its oral groove to the mouth. Thus any stimulus that can be transmitted by such a stream, as for instance a chemical or heat and cold, comes into contact with the

anterior end and oral groove earlier than with any other part of the body. These are, moreover, the most sensitive parts of the body. Now when Paramecium thus encounters a stimulating agent, it appears that these are the parts of the body that react. The animal at first swims backward, circling at the same time toward the aboral side. After a moment the animal swims forward again, still turning toward the aboral side. The direction of its course is thus changed, and the animal continues in this new direction if it does not again encounter the stimulating agent; but if it does, it goes through the same motor reaction again, by swimming backward, turning toward the aboral side and then swimming forward once more. This process is repeated until the animal is finally brought beyond the range of the stimulus. The animal invariably turns toward the aboral side, even when this at first brings it more immediately into the region of the stimulus than it had been before. The author aptly names this, orientation by trial and error. And he further finds that this is the only manner of orientation observable in Paramecia, and that this fact is utterly at variance with the current theories of thermotaxis.

The conclusions are based on extended observations of Paramecium, and they are confirmed by entirely concordant observations of the other ciliate infusoria, *Oxytricha fallax, O. aeruginosa, Stylonychia mytilus, Stentor caeruleus, Spirostomum ambiguum* and *Bursaria truncatella*. Both heat and cold were tried as stimuli in nearly all the cases.

Second Paper. REACTIONS TO LIGHT IN CILIATE FLAGELLATES.

The reaction of the ciliate, Stentor, to light is the same as its reation to heat and cold. It stops or swims backward a short distance, then turns toward the aboral side, and resumes its forward motion. "This is the reaction which is produced by strong mechanical stimuli, by heat, and by chemical stimuli, acting upon the anterior end or upon the body as a whole." And here too, the reaction is the same, although at first the animal may be brought directly into the stimulus which it is seeking to avoid. "*The direction of turning is thus determined by an internal factor*—the structure of the body." The orientation is not governed by the direction of the light-rays (contra LOEB), nor yet by the part of the body that receives the stimulation (contra VERWORN and others). Indeed the response is not altered if the stimulus acts on all parts of the body at once.

The flagellates normally swim in a spiral path, continually swerving toward that side which bears the larger "lip" and the eye, the so-called dorsal side. While swimming toward a source of light *Euglena viridis* will, if suddenly the illumination is decreased or greatly in-

creased, swerve more rapidly toward the dorsal side and swim less rapidly forward, and then proceed as before but in a new direction. In course of this the anterior end of the body describes a circle while the posterior end moves but little and is virtually a pivot for the freer end. "The reaction which occurs when the illumination is changed is really an accentuation of a certain feature of the usual movements." Now if the change in illumination has been slight, the animal will slowly resume its forward movement swerving less noticeably toward the dorsal side, so that presently it will be moving along its former spiral course. But if the modified illumination is now too great, the animal while describing the pivotal movement will find its anterior (and more sensitive) end turned toward the light at some points of its circular course and away from it at others; since now the light is supraoptimal, the animal will commence the forward movement while its anterior end is turned from the light, so that its new spiral course as it is gradually resumed will be directed at least somewhat away from the source of light. If this change in course is not sufficient to make the animal recede from the source of light, the animal will either tack again in the same way as before, or else change its orientation gradually but in a way very comparable with the previous. That is, the organism will swerve farther than normally toward the dorsal side and this will cause its anterior end to point successively in many different directions. In some of these positions the anterior end is directed more nearly toward the source of light, in other positions farther away from it. In the latter case the swinging toward the dorsal side becomes less marked; hence the succeeding phase of the swing, which carries the anterior end toward the light, is less pronounced; The anterior end therefore does not swing so far in the direction toward the light as in the preceding phase it swung away from the light. But as a result of such swerving as does occur the anterior end is now directed more away from the source of light than before. Thus this gradual change of orientation is effected by means of the same principles as the former, more sudden change. In either case the direction of the rays of light is not a determining feature, and the orientation is effected by a definite sort of "motor response."

This description applies to the movements of orientation of ciliates and flagellates in general. The ciliate studied was *Stentor caeruleus;* the flagellates were *Euglena viridis, Cryptomonas ovata* (sometimes called *Chilomonas ovata*), and a species of *Chlamydomonas.*

Third Paper. REACTIONS TO STIMULI IN CERTAIN ROTIFERA.

The author studies the Rotatoria, a group of metazoa much re-

sembling the infusoria in their mode of life, in order to find whether the reaction method of the metazoa differs radically in character from that of infusoria. The following free-swimming Rotifera, which progress through the water in the same manner as the ciliate infusoria, were studied; several species of the Rattulidae and of the Cathypnadae, two or three species of Euchlanis, *Ploesoma lenticulare*, *Anuroea cochlearis*, and *Brachionus pala*. The stimuli used were chemicals, heat, light, and the constant electric current. The reactions of all these Rotifera are essentially the same as those of the ciliate infusoria.

Fourth Paper. THE THEORY OF TROPISMS.

This paper forms an admirable summary and theoretical discussion of the undoubtedly careful and exact observations described in the foregoing three papers. And it is to be said, further, that in each paper the author evinces the rare combination of qualities—a lively theoretical interest combined with the power of impartial observation.

The paper aims utterly to destroy the theory of the several "-taxes." Firstly, the theory of LOEB and others that the direction of ray (in light and electricity) is the determining factor in orienentation is untenable, because all the organisms studied react only by swerving toward a structurally defined side of their own bodies, even although this movement causes them to turn directly toward the rays that they seek to avoid. The theory that the intensity of stimulation effects orientation by a local effect on such parts of the body as it reaches is untenable, because in many, if indeed not most, organisms the anterior end is the only part sensitive enough to be effected by the stimuli (that is, the threshold of orientation is the threshold of stimulation of the anterior end); and because, as in the previous case, the response is invariably a perfectly definite "motor reaction" toward an anatomically defined side of the body of the organism. The defenders of the theory of tropisms will hardly call in question Professor JENNINGS' patently exact and unbiased observations, nor his methods, which are of the most careful, nor yet the range of organisms which he has chosen to study, which is far greater than that of any other individual experimenter. But they may possibly ask Professor JENNINGS what it is if not intensity of stimulation that causes the organisms, while circling on their anterior ends as pivots, to dart forward more or less suddenly at that point of the circle where the anterior end receives least of the undesirable stimulus; and if this cause is the intensity, whether his observations have not demonstrated a phototaxis of the anterior end. But even if this were to be the case, Professor JENNINGS would have effected a most important refinement on the old

theory, and contributed vastly to our knowledge of the behavior of lower organisms.

Fifth Paper. PHYSIOLOGICAL STATES AS DETERMINING FACTORS IN THE BEHAVIOR OF LOWER ORGANISMS.

In unicellular organisms as in multicellular the forms of reaction to stimuli exhibited clearly indicate the importance of internal factors (physiological states) as determining conditions. "To the same stimuli, under the same external conditions, the same individuals react at different times in radically different ways, (thus) showing the existence of different physiological states of the organism, which determine the nature of the reactions," p. 126. JENNINGS adduces numerous observations of the behavior of various unicellular organisms and flatworms in proof of the falsity of the prevalent notion that the reactions of these animals are determined almost wholly by external conditions. As a matter of fact all organisms, so far as reactions are concerned, are influenced by both external and internal conditions, and it is only because of the apparent invariableness of the reactions of the lower animals that they are so commonly spoken of as automata which are at the mercy of their surroundings in a quite different way than are the higher animals.

The paper serves the good purpose of calling attention to the fact that reactions are more often determined by the total state of the organism than by the local action of a stimulus.

Sixth Paper. THE MOVEMENTS AND REACTIONS OF AMŒBA.

This paper, like the earlier ones of the volume, rudely shakes the foundations of certain current theories of reaction, and it totally destroys certain explanations of the reactions of simple organisms which have been pretty generally accepted by physiologists. Unfortunately for the peace of mind of certain of the earlier investigators of the movements and reactions of Amœba, the author was not satisfied to accept what had already been done in this field of research as the basis of his work. He chose instead to begin at the beginning and to attempt to verify the descriptions already given.

RHUMBLER and BÜTSCHLI state that in the normal locomotion of Amœba there is a forward moving current of endosarc in the middle axis which flows outward at the anterior end of the organism, then backward along the surface. According to these physiologists, the protoplasmic currents within a moving Amœba are essentially like the movements produced in a drop of water by lowering the surface tension at some point. The axial current moves toward the point of decreased tension. Consequently RHUMBLER and BÜTSCHLI conclude

that the movements of Amœba are due to changes in surface tension. JENNINGS, on the basis of careful observation of the movements of several species of Amœba, states that there are no side or backward currents, but that the process occurs as follows : "In an advancing Amœba substance flows forward on the upper surface, rolls over at the anterior edge, coming in contact with the substratum, then remains quiet until the body of the Amœba has passed over it. It then moves upward at the posterior end, and forward again on the upper surface, continuing in rotation as long as the Amœba continues to progress. The motion of the upper surface is congruent with that of the endosarc, the two forming a single stream " p. 148.

Accurate and detailed descriptions are given of the processes of formation and withdrawal of pseudopodia, and it is shown that contractility is a capacity of the ectosarc. "Altogether, then, our results lead us to look upon Amœba as an elastic and contractile sac, containing fluid. In locomotion one side actively stretches out, becomes attached to the substratum, and draws the remainder of the sac after it in a rolling movement. The primary phenomena are the stretching out of one side, the elasticity, and the contractility of the outer layer" p. 172.

Under the subject of reactions, the author presents the results of extensive studies of the influence of different stimuli upon Amœba. He distinguishes three classes of reaction : the positive, the negative, and a complex feeding reaction. Several interesting instances of the pursuit of food are cited in support of the author's opinion that the behavior is by no means so simple and uniform as is commonly supposed.

After redescribing the protoplasmic movements of Amœba in the light of his own observations, the author discusses the physics of locomotion with results which may most fitly be expressed in his own words. "Putting all our results together we must conclude that the movements and reactions of Amœba have as yet by no means been resolved into their physical components. Amœba is a drop of fluid which moves in its usual locomotion in much the same way as inorganic drops move under the influence of similarly directed forces. But what these forces are is by no means clear. When we take into consideration the currents as they actually exist, local decrease in surface tension breaks down completely as an explanation for the locomotion and other movements. The locomotion taken by itself might be explained as due to the adhesion of the fluid protoplasm to solids,

taken in connection with the surface tension of the fluids, but this explanation fails when we consider the formation of free pseudopodia, and discover that all the processes concerned in locomotion can take place without adhesion to the substratum." 225.

Seventh Paper. THE METHOD OF TRIAL AND ERROR IN THE BEHAVIOR OF LOWER ORGANISMS.

In higher animals we speak of *learning* by the method of trial and error, and in unicellular organisms we may speak of the trial and error method of reaction. In the former instance the animal when first confronted by a certain situation exhibits a number of reactions; one of these reactions brings satisfaction and therewith the trial reactions cease. The next time the same situation is presented the animal, if it has learned, omits the useless or harmful trials and performs only the appropriate reaction. In the latter instance, namely, in case of unicellular organisms, each re-presentation of the situation brings about, so far as yet observed, the same sort of trial and error series of reactions. Whereas the mammals after a number of experiences omit the majority of the trials, the protozoa apparently have to go through the whole gamut of tests each time.

Trial may then be defined as the process of testing different portions of the environment, and error is descriptive of those trials which result in negative reaction. Now, the problem proposed by the author is, How is error distinguished by the organism? "In ourselves the stimuli which induce the negative reaction bring about the subjective state known as pain, and popularly we consider that the drawing back is due to pain. Is there ground for this view?" p. 248. This problem, JENNINGS insists, is one throughout the animal series.

Finally, the method of trial and error which the author believes to be the prevalent mode of reaction among lower organisms is not in agreement with the principles of reaction which are at the bottom of the tropism schema. For the tropism is a fixed way of reacting in response to a certain stimulus, and it has no place for the trials which have been demonstrated to occur.

Whether this is fair to the advocates of the tropism formulae for reactions would be hard to say. Certainly some of them will at once contend that JENNINGS by merely breaking up the stereotyped reaction into a number of parts has not altered the nature of the reaction.

The author's insistence throughout this volume upon the importance of internal conditions in lower organisms is certainly justified by the facts he presents.

That this series of papers is fundamentally important for the science of animal behavior is obvious.

E. B. H. AND R. M. Y.

Hornaday, Wm. T. The American Natural History. *New York, Scribner's Sons*, 1904, xxv + 449.

A popular natural history which contains much interesting and valuable information concerning American animals. The work is splendidly illustrated and pleasingly written. It should be of considerable value as a means of arousing interest in animals and stimulating to a study of their characteristics.

R. M. Y.

Cohn, Paul. Gemütserregungen und Krankheiten. *Berlin, Vogel und Kreienbrink*, 1903, pp. 148.

The book contains a study of the nature and localization of emotions. The first part deals with the physiological accompaniments of feelings and emotions, the second with their pathological effects, and the third gives hints for a prophylaxis. The author adopts the theory that all feelings can be reduced to organic sensations of the body and of the brain. He professes a general disdain for all previous work, which he claims to be too speculative, and he acknowledges NIETZSCHE as his only predecessor. None of the modern inquiries into the nature of feelings is mentioned, and the experimental studies of the physiological influence of feelings are utterly ignored.

F. M. URBAN.

Putnam, J. J. The Value of the Physiological Principle in the Study of Neurology. *Am. Medicine*, 1904, **8**, No. 25, 1051-1056.

Dr. PUTNAM's address before the section of Neurology of the International Congress of Arts and Sciences at St. Louis is published in full in *American Medicine*, as cited above, and simultaneously in the *Boston Medical and Surgical Journal*. The contrast is sharply drawn between VIRCHOW's "Anatomical Principle in the Study of Disease" and the attempt to localize morbid processes on the one hand, and on the other hand the morbid process as maladjustment. "No anatomical research can pierce to the secret of broken coördinations, and yet it is in these that a great part of disease begins, or comes eventally to consist." "Every organism, whether we call it diseased or well, presents itself to our view as a web of interwoven 'energies,' which in order to study them by anatomic means, we must break artificially into fragments that have, in reality, no correspondingly separate existence." This is a point of view which has its application in normal function, as well as in pathology.

C. J. H.

Halben, R. Theoretisches über die Bedeutung des Pigmentes für den Sehakt der Wirbellosen, speciell der Protozoen. *Biol. Centralbl.*, 1904, **24**, No. 8, 283-288.

An argument, against HESSE, for the importance of pigment in light perception. A foot-note contains a discussion of the nature of light, which should be read by all students of phototaxis.   G. W.

Weysse, Arthur W. Notes on Animal Behavior. *Science*, N. S., 1904, **19**, No. 495, 955-957.

Discusses certain actions of a black-and-tan terrier, which by many would be taken to exhibit a high degree of intelligence. WEYSSE shows how, in these particular cases, much simpler explanations can be given, based on the ordinary habits of the dog.

LEON J. COLE.

Scott, William E. D. The Inheritance of Song in Passerine Birds. Remarks on the Development of Song in the Rose-breasted Grosbeak, Zamelodia ludoviciana (Linnæus), and the Meadowlark, Sturnella magna (Linnæus). *Science*, N. S., 1904, **19**, No. 95, 957-959 ; Further Observations on the Development of Song and Nest-building in Hand-reared Rose-breasted Grosbeaks, Zamelodia ludoviciana (Linnæus). *Science*, N. S., 1904, **20**, No. 504, 282-283.

Rose-breasted grosbeaks were taken from the nest when five days old and after being kept in confinement until about eight months old they sang a song that "could not be referred to the rose-breasted grosbeak." Meadowlarks taken from the nest and kept in confinement, besides having a peculiar song of their own, accompanied by a "parade or dance," also imitated the songs of some German "blackbirds" (*Merula merula*) with which they were associated. The conclusion is "that birds are influenced in their early lives very strongly by any noise that arrests their attention, even in a wild state, and that their propensity to imitate and differentiate their normal methods of song is greatly exaggerated under the artificial state wherein they live when in confinement."

In the second paper the observations of the first are confirmed. The songs of the grosbeaks came to resemble that of a green bulbul (*Chloropsis hardwickii*) which was kept in an adjacent cage. In May the grosbeaks attempted to build a nest in the cage, but although supplied with materials, they were unable to construct a nest for themselves, though they added a lining of feathers and cowhair to artificial nests that were supplied.   LEON J. COLE.

THE MORPHOLOGY OF THE VERTEBRATE HEAD FROM THE VIEWPOINT OF THE FUNCTIONAL DIVISIONS OF THE NERVOUS SYSTEM.[1]

By J. B. Johnston.

With Plates I to IV.

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I. Introduction.

a. Nature of the unsettled problems.

Shall we consider vertebrates as animals possessing a high degree of cephalization from their first appearace ?. The structure of their near relatives, Amphioxus and Ascidians, is against this view. The structural relations of vertebrates and invertebrates indicate that the ancestors of the vertebrates were segmented invertebrates in which the process of cephalization had not gone very far. Even within typical vertebrates evidence is not lacking that the special sense organs of the head were late to appear; that the branchial apparatus was at one time more extensive, reaching into what is now the trunk ; that the nerves of the branchial region once had a more simple segmental arrangement ; and that in the brain itself the several regions were once less highly specialized than at present. If Amphioxus be considered, the presence of true nephridia (41) in the head and the slight specialization in the head region seem to relate this "lowest vertebrate" with invertebrates rather far down the scale.

If, then, the ancestral vertebrate had only a slight head development, it is evident that the interpretation of the special organs of the head of typical vertebrates is to be reached by a study of their structure, function, and phylogenetic history, with a view to tracing them back to their unspecialized beginnings. When each organ has thus been followed back to its ancestral condition we shall have reduced the vertebrate head to terms—not of the trunk, but of a more simple condition which underlies both head and trunk. Such is the real problem of head morphology as the writer understands it.

The central difficulty in framing such a conception of the head is the matter of segmentation. Head specialization has

gone so far that in known vertebrates few or no segments con-
tain, even in the form of embryonic vestiges, all of the struc-
tures which were typically present in the anterior segments of
the ancestral vertebrates. On this account it has been ex-
tremely difficult to reconstruct complete segments, even where
our information as to existing structures is apparently complete.
Not only have certain organs with their nerves and nerve cen-
ters undergone reduction, or disappeared, but new organs have
arisen and old ones have been modified so that new nerves and
centers have replaced or overshadowed old ones. Furthermore
it appears that as a result of these changes various organs and
nerves have been displaced from their proper segments by the
crowding of lately formed highly developed structures. We
are met by a present condition which is the result of processes
of reduction and disappearance, modification and growth, and
shifting of position of organs whose real segmental relations
are to be discovered only by tracing them back to their primi-
tive condition. Thus the deciphering of the segmental relations,
depending, as it does, on the proper interpretation of the
homology and phylogenetic history of all the organs, will carry
with it the solution of the major problems of head morphology.
It must not be hoped that the last word upon any of these
problems can be said at once. The data are yet too meager
for the solution of this greatest problem of the evolution of
animal structure, in spite of the efforts of a large number of
workers directed to it during several decades. What the writer
hopes to do in the present paper is: first to apply a new method
for the interpretation of head segmentation which recent work
on the nervous system has made possible ; and second to point
the way to some profitable lines of investigation.

b. Nerve components.

The function of the nervous system to coördinate and
direct all the organs of the body requires a definite and con-
stant relation of its constituent parts to the several tissues and
organs. The structural and functional relationships within the
organism become impressed upon the nervous system and the

arrangement of its cells and fibers serves as a guide to these relationships. Further, by a study of its residual or vestigeal structures and its ontogeny in various classes of animals we gain hints of many of the past relationships between the other organs. On account of its function as a go-between, the nervous system becomes for us an interpreter. The truth of this has long been realized but it has become of practical value only since the work of OSBORN, ALLIS and EWART led the way to the development of the theory of nerve components by STRONG, HERRICK and others. According to this theory, those fibers in the cranial nerves which supply the same kind of end organs enter the same or comparable regions in the brain. For example, all general cutaneous fibers (free nerve endings in the skin) enter the spinal V tract in the brain and the dorsal tracts in the cord. It happens that a nerve trunk is commonly composed of two or more sets or kinds of fibers. All those fibers in the several nerves which have the same central and peripheral connections are said to belong to one and the same *system of nerve components.*

Although this theory concerns itself directly with the analysis of peripheral nerve trunks, its value rests upon the existence of functionally distinct types of end organs on the one hand and distinct nerve centers in the brain on the other hand. The analysis of nerve trunks into nerve components necessarily implies the analysis of the nervous system as a whole from the same point of view, that is, on the basis of function. In this new way of looking at the nervous system the brain, which from the standpoint of structure has always been regarded as the most complex and obscure portion, becomes the most illuminating—and this just because of its complex relations. Three considerations are important in this connection. First, the reasoning on which the theory of nerve components rested could not be made good unless it was shown that the fibers of two components were independent in their central relations. For example, unless it were clearly shown that the centers in which the general cutaneous fibers end are structurally and hence functionally distinct from those into which sensory fibers

from the mucosae enter, we could not assume that the observed
distinct peripheral course of these two sets of fibers had any
functional significance. If it had proved that the fibers from
the skin and those from the mucosae entered the same centers
and had the same primary and secondary connections within
the brain, we should have been compelled to conclude that sen-
sory impulses from the skin and those from the mucosae would
bring about the same reactions. As a matter of fact it has
proved not only that the primary centers of these two sets of
fibers are distinct, but that their secondary and tertiary fiber
tracts remain separate and distinct. Hence it may be concluded
that *any* fiber bringing impulses into the cutaneous center must
set up reactions which *characteristically* follow cutaneous stimu-
lation. The same reasoning may and must be applied to each
system of nerve components. Furthermore, the central relations
of any system of nerve components when certainly known serve
as a starting point from which one may reason back with perfect
validity to the homology and probable function of the organs in-
nervated by that system. To illustrate by a case which is
still under some dispute, it was by this method that the writer
concluded that the end buds belonged to the visceral sensory
system before their gustatory function had been proved by ex-
tended experiment (67, 49).

Second, the brain sometimes gives clues to primitive func-
tional relationships of which the peripheral nerves no longer
bear traces. In certain segments of the head this or that nerve
component is wholly lacking owing to the disappearance of the
structure which it originally innervated. Yet in these same
segments the brain retains in some cases the center or column
which this component should enter. A simple example of
this is the presence of the somatic motor column throughout
the medulla oblongata even in those forms in which several
segments are without any other vestige of ventral motor
nerves. The cases of the cerebellum and tectum opticum have
been considered at some length in previous papers (67, 68, 69,
70), and these and other cases of the same sort will be treated
further in the present paper. Wherever the brain contains a

representative of one of the primary columns there is presumptive evidence that in the primitive vertebrate the corresponding peripheral structures were present in the same segment.

Third, in cases of extreme modification of other systems of organs and of the peripheral nervous system the brain retains structural features which serve to point the way to the interpretation of new structures. The changes of structure and function, so far as yet observed, are less fundamental than the primitive functional divisions of the nervous system. ''New structures'' arise as modifications within one division, not by structures belonging to one functional division taking on functions belonging to another division. It does not happen, for example, that cutaneous structures (sense organs, components, centers, or fiber tracts) are so modified as to serve visceral functions, or vice versa. This conservatism of the brain aids in the interpretation of structures which otherwise would be very difficult to understand. By this method of reasoning the evidence that the ear is a part of the lateral line system has been completed, and it has been shown that both ear and lateral line system have arisen by modification within the primitive general cutaneous division of the nervous system. The principle will be applied in this paper for the interpretation of the eye and other organs. It is perhaps needless to say that this principle has been only slightly tested and it is not yet known whether it is universally true. While it promises to be of great value, it must be used with extreme caution.

c. Functional divisions of the nervous system.

Such considerations as the above led the writer some time since to offer a scheme of the primitive functional divisions of the nervous system. This theory is not only in accord with the theory of nerve components but is an extension of that theory so as to give due recognition to the central organ. It is unnecessary here to enter into explanations or arguments in support of this theory of functional divisions beyond the matter contained in previous papers (69, 70). Here a concise outline of the functional divisions is given, with their subdivisions and

constituent elements. This outline differs from the one previously published chiefly in that the visual and olfactory organs and the sympathetic system are assigned to definite places in the scheme, a thing which was not attempted before.

A. Somatic sensory division.
    1. General cutaneous subdivision. Consists of :
        free nerve endings in the skin,
        general cutaneous system of components,
        dorsal tracts of the cord, spinal V tract in the medulla oblongata, together with their accompanying nuclei : the dorsal horn, nucleus funiculi, nucleus trigemini spinalis, acusticum and cerebellum,
        secondary tracts and centers : internal and external arcuate fibers forming the tractus spino- and bulbo-tectalis (fillet), tectum opticum, colliculus and other nuclei,
        tertiary tracts to motor nuclei and coördinating centers.
    2. Special cutaneous subdivision. Consists of :
        neuromasts (acustico-lateral sense organs),
        neuromast components,
        spinal VIII tract and nucleus, nucleus funiculi, acusticum, cerebellum,
        secondary tracts and centers and tertiary tracts as in 1,
        the cochlea, its nerve and centers in higher vertebrates.
    3. Special sense organs belonging to the somatic sensory division.
        lateral eyes. Consist of :
        retina, which includes the equivalent of sensory ganglion, nerve component, and primary brain center,
        optic tract and tectum opticum corresponding to the secondary tracts and centers of the cutaneous subdivision.
        pineal eyes. (Compare Sec. 13 below).
B. Splanchnic sensory division.
    1. General visceral subdivision. Consists of :
        free nerve endings in the mucosae,
        fasciculus communis system of components,
        CLARKE'S column or its equivalent, nucleus commissuralis CAJAL, lobus vagi, and lobus facialis,
        secondary vagus tract and its continuation in the cord, = the direct cerebellar tract in higher forms,
        secondary vagus nucleus, = end nucleus of direct cerebellar tract in the vermis of higher forms,
        tertiary tracts not well known ; part probably run to the thalamus or hypothalamus in lower vertebrates.
    2. Special visceral subdivision. Consists of :
        end buds (taste buds),
        components and central nuclei and tracts not yet distinguished from those of the general visceral subdivision.
    3. Special sense organ belonging to the splanchnic sensory division.
        Consists of : olfactory epithelium and nerve, bulbus olfactorius, tractus

olfactorius, area olfactoria, and tertiary tracts to coördinating cen-
ters in the diencephalon.

4. Sympathetic system, afferent portion. An outgrowth or offshoot from
splanchnic sensory ganglia which reaches a high specialization in
the vertebrate series. Consists of simple splanchnic sensory com-
ponent fibers and of ganglion cells which together with the efferent
portion form a somewhat complete or independent system.

C. Somatic motor division. Consists of:

ventral horn of the cord, nuclei of origin of Nn. XII, VI, IV, III, and
nucleus of somatic motor fasciculus,

motor components in ventral roots supplying musculature derived from
the somites.

D. Splanchnic motor division. Consists of:

1. Motor nuclei in lateral horn or intermediate zone of the cord and corre-
sponding region of the medulla oblongata,

motor component in dorsal and ventral roots supplying musculature
derived from lateral mesoderm.

2. Sympathetic system, efferent portion. Consists of simple splanchnic
motor component fibers (?) and of ganglion cells and fibers con-
cerned with glandular secretion, etc.

In addition to the structures included in the above outline
there are certain brain centers which with their fiber tracts
probably serve functions of coördination between the four pri-
mary divisions. It is not at present possible to define exactly
each of the functional divisions with its secondary tracts and
centers, or to understand fully the relations of the coördinating
structures even in the simplest vertebrate brains. Some con-
tribution upon this subject will be found in the following pages.
With one important exception (see Sec. 15), however, sufficient
is already known for our present needs in discussing the homol-
ogy and segmental arrangement of the organs of the head.

d.   Bearing upon the subject of head morphology.

The essence of the theory of functional divisions is this:
Each system of organs in the vertebrate body is connected by
definite fiber paths with certain nerve centers which direct and
coördinate the actions of those organs. Those peripheral and
central nervous structures which are related to a given set of
organs form a structurally distinct portion or division of the
nervous system extending through the length of the animal
and represented in successive segments by serially homologous

structures. The coördination of action between systems of organs having different functions is effected through central connections between these functional divisions. To what extent direct, simple or short connections between the centers of different divisions serve this purpose is not yet fully understood. But at least in some cases it appears that the divisions remain separate as far as their tertiary tracts and coördination is effected through special structures. It follows that these *longitudinal* divisions of the nervous system are fundamental in character and are much more significant than the transverse divisions (fore-brain, hind-brain). Each functional division is represented in successive segments by serially homologous organs, while the transverse divisions of the brain are for the most part merely mass portions which have little segmental value. It remains to show the bearing of this view of the nervous system upon the problems of head morphology.

A serious attempt can no longer be made to determine the segments of the vertebrate head by a study of the structure and development of one system of organs alone or chiefly. The method is limited because the set of organs selected for study is not coextensive with the whole organism. One quasi exception to this exists. Owing to the necessities of the case the nervous system is represented in every segment of the organism. Each system of organs has its representation in the nervous system; *if we can read aright*, in the segmentation of the nervous system we read the segmentation of the organism.

Reasoning in some such way as this, some authors have attempted to determine the segmentation of the head by means of the central nervous system alone. While the central nervous system at an early stage of development may show the *number* of segments of the whole head, it can show little as to the relations and arrangement of other organs, what organs are present in given segments, etc. Further, any study of segmentation from the nervous system alone is met by the difficulty that, although some part of the nervous system must be present in each segment, one or more of its main divisions may be absent. What part of the nervous system is represented in

a given segment depends upon what other organs are present in that segment. This very obstacle suggests the way in which the nervous system may be used with special profit, namely, as a key to the interpretation of the facts secured by the study of the other organs. From the point of view given by the theory of functional divisions we get an advantage in the study of head segmentation which may be stated as follows. The scheme of functional divisions serves to define a complete or typical segment and so enables us to determine whether all the proper parts are present in a given segment. A complete segment of head or trunk of a typical vertebrate should consist of : (a) derivatives from the ectoderm (skin), from the entoderm (gut), from the dorsal mesoderm (somatic musculature), and from the lateral mesoderm (visceral musculature), and (b) the corresponding four main divisions of the nervous system : somatic sensory, splanchnic sensory, somatic motor, splanchnic motor. With this clearly in mind we shall be able to say when a segment is complete, when incomplete, what constituent has disappeared, and for what probable reason. When we can say this for each segment of the head the problem of segmentation will be solved.

In order to proceed by this method it will be necessary first to give a summary of what has been established by previous workers on the various systems of organs. It is not the intention to give a critical review of the literature of head segmentation or to undertake the discussion of disputed points; but only to give a brief statement of the facts that may be used in attempting to reconstruct the primitive vertebrate head. It is believed that a constructive effort aiming to correlate all the well established facts from a new point of view is more valuable than criticism or the weighing of one set of facts over against another.

2. Number and relations of mesodermic somites.

Since the work of later authors has given strong confirmation to the main results of VAN WIJHE (119) we may use his nomenclature in referring to the somites.

a.   A continuous series of mesodermic somites appears in early embryos of lower vertebrates.   The earliest somite to appear lies in the neck region and others are formed progressively forward and backward from this point.   The order of their appearance and the continuity of the series justifies the conclusion that the somites of head and trunk belong to a single series.

b.   That somite of this series which VAN WIJHE numbered somite 2 always lies dorsal to and is continuous with the mandibular arch.   The relation of the succeeding somites to the branchial arches is more or less complicated.   See Sec. 3 below.

c.   In front of this lie two somites, the praemandibular, or somite 1 of VAN WIJHE, and the anterior head cavity of PLATT (119, 124, 106, 57).

d.   Somites 1, 2 and 3 give rise to the eye muscles in all vertebrates.

e.   The anterior head cavity of PLATT never persists.

The question whether somite 1 is composed wholly of dorsal mesoderm and whether the mesoderm anterior to it is dorsal or lateral may be discussed here.   It is a question which can scarcely be answered by direct observation.   The exact condition of the mesoderm in this region in cyclostomes is uncertain.   KUPFFER has described and figured for Ammocoetes (78) well developed vestiges of branchial and aortic arches surrounding the hypophysial canal, the relationships being the same as in the pharyngeal region; but this has not been confirmed.   His argument from the position of these arches that the (whole of the) praemandibular mesoderm constitutes a lateral or branchiomeric segment is negatived by the fact (stated by himself also) that the dorsal part of this mesoderm forms an eye muscle which is innervated by a true ventral nerve in all vertebrates.   In selachians also, where the mesoderm is better preserved, the embryonic history fails to give any positive evidence of the existence of branchial arch mesoderm in front of the mandibular arch.

One important consideration is to noticed here, however, which has a bearing on the whole problem of segmentation. It is that in the anterior part of the head in all lower verte-

brates the mesoderm is completely segmented transversely at an early stage and that the dorsal part (somite) is not clearly separated from the lateral (branchiomere) at any time. This is always true of somite 2 and the mandibular arch. In sela-chians the transverse segmentation precedes the separation of somite 3 from the hyoid arch. Even in amphibia (Amblystoma)[1] the hyoid arch is connected with somite 3 and is separately split off from the entoderm, having had no connection with the following lateral mesoderm. Further, the anterior head somites develop as gut pouches in cyclostomes in reminiscence of the mode of mesoderm formation in Amphioxus. The late con-nection of somite 1 with the entoderm is a slight indication of the same thing in selachians (57, 17). In all these respects the head mesoderm presents primitive conditions. Now if it be thought that one or more gill slits and arches have ever existed in front of the present mouth, it is in no way unrea-sonable to suppose that some vestige of the branchial arches (lateral mesoderm) may be retained indistinguishably connected with somite 1 and the anterior head cavity, just as the mandib-ular arch is attached to somite 2 without definite boundary line. The fate of such lateral mesoderm other than mesen-chyme formation is not known.

f. Somite 4 lies mesial to or slightly caudal to the audi-tory vesicle during its formation and immediately in front of the ganglion of the glossopharyngeus. This is consequently often designated as the first postauditory somite.

g. More or fewer of the postauditory somites become re-duced or disappear during development. Petromyzon forms an exception to this and the conditions there as described by KOLTZOFF (76) are sufficiently important to be reported in this connection. Somites 4 and 5 become divided into mesial and lateral parts which are completely separated in somite 4, but in somite 5 remain connected by a slender bridge. The mesial part of both of these somites lies close to the chorda and later

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[1] References to Amblystoma are based on my own observations not before published.

disappears, that of somite 5 the more slowly. The ganglion of the glossopharyngeus crowds outward, downward and forward between the mesial and lateral parts of somite 4, while the vagus ganglion assumes the same relation to somite 5. The lateral part of somite 4 sends dorsal and ventral buds forward above and below the ear. Somite 5 sends a dorsal bud above the ear and similar buds follow from somite 6 and perhaps somite 7. These dorsal buds of somites 4, 5, 6 (and 7) form the continuation of the body muscles on the top of the head as far forward as the olfactory pit. The great extent anteriorly of this musculature in Petromyzon is connected with the buccal apparatus. Such dorso-lateral portions are found only in somewhat more caudal somites in selachians : somite 7 in Acanthias (58), and Pristiurus (119); somite 8 in Spinax (12) somite 12 in Torpedo (112). The absence of this lateral part in the region of the cranial nerves accounts (SEWERTZOFF, KOLTZOFF) for the position of these nerves outside the myotomes. In Petromyzon the lateral portions of the myotomes cover the cranial ganglia just as the trunk myotomes cover the spinal ganglia in all vertebrates. From this it seems that no somite completely disappears in Petromyzon but the myotomes of the adult represent the full quota of muscle segments.

h. Some of the myotomes in the caudal part of the head region send ventral muscle buds down behind the gills and forward ventrally to form the subbranchial musculature. In selachians this begins with myotome 8 or 9, in Petromyzon with myotome 10. It seems that the number of gills determines which myotome shall be the first to contribute to these muscles. As the number of gills decreases more anterior myotomes are able to send buds into the subbranchial region.

i. Each of the myotomes is supplied by a true ventral nerve root. The number of these roots in the postauditory region of the adult depends on the number of persistent myotomes, and in the embryo transient roots appear corresponding to transient myotomes. A more detailed treatment of this relation will be given farther on (Sec. 12).

j. There appears in all gnathostomes a variable amount of

shifting forward of myotomes in the neck region following upon the reduction of postauditory myotomes.

k. The number of somites in the head can not be stated for vertebrates in general, since the caudal limit of the head varies from group to group. This will be further discussed below (Sec. 12).

3. Branchial apparatus and lateral musculature.

The position of the gill slits with reference to the' myotomes has been one of the most vexed and vexing questions of head morphology. The most direct and natural assumption is that dorsal and lateral mesoderm had primitively a common segmentation and that the gill slits were situated between the mesodermic segments. Each branchial arch would thus be continuous dorsally with a myotome. This condition, if it ever existed throughout the branchial region, is now preserved only in the case of the mandibular arch and somite 2, and in some forms in the case of somite 3 and the hyoid arch. Caudally to this the branchial arches bear no definite relation to the somites, in most vertebrates. This is certainly due in part at least to the reduction and shifting of postauditory myotomes mentioned above and to the growth and expansion of the branchial apparatus itself. These two processes result in a shifting forward of myotomes and backward of gill pouches and arches, not only in relation to one another but also in relation to other organs (58, 60, 12). Since such shifting is observed in the ontogeny it may be expected that the primitive condition would be found in very young embryos. In most vertebrates, however, such a direct correspondence between somites and branchial arches as was supposed above does not exist at the time when the structures in question are formed. These facts have led some authors to the conclusion that the branchial segmentation is independent of that of the dorsal mesoderm.

The writer is unable to harmonize this conclusion with the arrangement of the cranial nerves. Also, this conception implies a distinct and divergent dorsal and ventral segmentation for the typical vertebrate: the mesodermic segmentation proper

extends only to the dorsal mesoderm, the segmentation of the lateral mesoderm is determined or dominated by the arrangement of the gills. Aside from the fact that this would scarcely be expected when we consider the character of invertebrate segmentation, the implications are inconsistent with the facts of segmentation in Amphioxus. Here the whole mesoderm is at first segmented and the lateral segments secondarily fuse into continuous lateral plates. A reminiscence of this is preserved, as we have seen above, in the head mesoderm of cyclostomes, selachians, and amphibia. If this be taken to indicate the primitive condition in vertebrates, then the idea of an independent branchial segmentation is hard to accept. It seems much more probable that the position of the entodermal gill pouches and of the ectodermal furrows was at first determined by the law of least resistance, the clefts between mesodermic segments offering favorable places for the breaking through of gill slits. The fact should not be lost sight of that in larval Amphioxus the branchial segmentation agrees with the mesodermic.

Fortunately we have in the work of KOLTZOFF on Petromyzon direct evidence bearing on this question. The primitive character of Petromyzon gives greater weight to this evidence. The mandibular arch is connected with somite 2 and the hyoid arch corresponds exactly to somite 3. The third, fourth and fifth visceral sacs on account of the thickness of the gut wall, are longer than the corresponding somites so that when five visceral sacs are formed the fifth lies beneath somite 9. While further visceral sacs are forming the gut wall is thinning out and the visceral sacs occupy less space. No visceral sacs are formed behind somite 9, but when the whole number, eight, are formed they occupy the space of eight somites. Immediately behind them somite (myotome) 10 sends down a ventral bud to enter the subbranchial musculature. Then at a later time the development and expansion of the gills carry them back until the last sac lies beneath somites 15-16, and by this movement the subbranchial muscle buds are cut apart from the myotomes 10, 11, etc. A complete correspondence between the branchial

segments and the somites is prevented in Petromyzon by the thickness of the gut wall in early stages. (It is possible that in ancestral vertebrates with less yolk a complete correspondence might have occurred.) With the using of the yolk and thinning out of the gut wall a numerical correspondence becomes possible, and it is important that the gill apparatus never extends beyond the point at which the first subbranchial muscle bud is to form ;—the point, that is to say, which should mark the caudal limit of the gills on the theory of complete correspondence of the two segmentations.

The investigation of other cyclostomes should throw further light on this important question. For the present, the many-sided indirect evidence which comes to impress one who attempts to frame a consistent account of head segmentation as a whole impel the writer to consider that the visceral apparatus and the dorsal mesoderm have a common segmentation. In accordance with this view the following statements may express the most probable conclusions regarding branchial segmentation and musculature.

a. There is essential correspondence between branchiomerism and mesomerism, the mandibular arch corresponding to somite 2.

b. This correspondence probably rests on a primitive complete segmentation of dorsal and lateral mesoderm, the gill slits being formed in the clefts between the mesodermic segments. Such a condition persists in the case of the mandibular and hyoid arches and the first and second visceral sacs in some vertebrates.

c. The lateral mesoderm forms visceral muscles moving the gill arches and the lower jaw. The nerves supplying muscles derived from the lateral mesoderm arise from the lateral motor nucleus in the medulla oblongata and are properly known as viscero-motor nerves.

d. Similarly the trapezius group of muscles are derived from the lateral mesoderm and are innervated by viscero-motor nerves. On this ground the pectoral girdle is perhaps to be regarded as a modified branchial arch. This is further supported

by the fact that in urodeles (Necturus, 108 ; Amblystoma) there are a large number of pouches in the wall of the gut in the trunk, segmentally arranged and resembling the gill pouches at the time of their formation. These are probably to be interpreted as vestiges of gill slits which formerly existed through a considerable portion of the trunk. Such seems to be the case in *Bdellostoma stouti,* where PRICE (109) has described thirty-five gill slits in the larva, the last 10-14 of which persist as the adult gills. The last gill slit lies in the same segment with the twenty-ninth spinal ganglion. The writer does not think that the great number of gills in Bdellostoma all belonged originally to the head and that their extension into the trunk is due to the shifting forward of trunk myotomes into the occipital region. The simpler explanation is much more probable ; namely, that there has been a reduction of the anterior gills on account of the parasitic life of the animal. The persistent gills really belong to the trunk and are homologous with the gut pouches seen in the trunk in urodeles.

e. The number of gill slits in existing vertebrates varies. At the so-called critical stage in Amphioxus there are 14, and this is usually regarded as the primary number for this animal. In *Bdellostoma stouti* 35 are formed, 10-14 persist ; in other species of Bdellostoma there are 6-7, 11-12, and 14 gill sacs ; in Petromyzon 8 larval, 7 adult ; in Heptanchus 7 ; in Hexanchus 6 ; in most selachians 5 ; in amphibia 4. It is not possible to draw from these figures any conclusion as to the typical number of gill slits for vertebrates. The writer thinks it very probable that the number of gills in primitive vertebrates was large and variable, even within the same species.

f. The lining of the pharynx is innervated by visceral sensory (fasciculus communis) components found in the VII, IX, and X cranial nerves.

4. *Segmentation of the central nervous system.*

Owing to numerous modifications of organs in the specialized head, the cranial nerves have become so changed from their primitive condition that the study of their segmental ar-

rangement has led to the most various results. Since the brain is a single continuous organ, the study of its segmentation would appear to be a comparatively simple matter. It has long been known that the spinal cord and medulla oblongata show a segmentation in early embryos which corresponds to the mesodermic segmentation. Indeed, the segments of the cord and brain were early regarded as merely the effect of mechanical pressure from the mesodermic segments. It has been clearly shown, however, that the transverse divisions are true segments, due to a definite arrangement of elements in the brain wall and often appearing before the mesodermic segmentation.

In spite of the apparent simplicity of the case, the study of the brain has led to scarcely better agreement as to the *number* of segments than the study of the cranial nerves. A summary of the findings of various workers is given in the papers by LOCY (125) and NEAL (97). In the hind brain, where the neuromeres are relatively distinct, they have been studied by numerous authors and in all classes of vertebrates. The disagreement among authors is due to the lack of a definite caudal limit to the brain and to differences in fixing upon the first neuromere to be assigned to the hind brain. The differences can be harmonized, however, by reference to the position of the nerve roots and ear, and by considering the shifting of nerve roots which has taken place. This discussion properly belongs to a future section (Sec. 9), but certain facts may be stated here. Accepting HOFFMANN'S enumeration which later work shows to be correct, rather than that of ORR and MCCLURE, there are in the hind brain of reptiles (ORR, HOFFMANN, MC-CLURE), birds (MCCLURE, HILL), and mammals (ZIMMERMANN) seven neuromeres; with the 2d, 4th, 6th and 7th of these are connected the Nn. V, VII-VIII, IX and X respectively. There are thus two neuromeres, one between the Nn. V and VII and one between the Nn. VII and IX, which are without nerve roots. For convenience such neuromeres will be referred to in the following pages as "blank" neuromeres. In fishes and amphibia there is but one blank neuromere, that between Nn. V and VII, and there is less agreement among authors as to the posi-

tion of nerve roots connected with the hind brain.   This will be discussed below (Sec. 9).

The segments lying in front of the cerebellum are variously interpreted owing to the comparatively early appearance of a segmentation corresponding to the permanent brain vesicles.   The segmentation of the brain tube in very early stages, before the formation of these vesicles, has been studied by ZIMMERMANN (124, rabbit, chick, selachians), WATERS (118, teleost), LOCY (125, selachians, with supplementry observations on the chick and amphibia), and HILL (52, teleost and chick). All these authors studied the neuromeres in all regions of the brain before the closure of the neural tube, in which stage those of the hind brain had already been seen by KUPFFER and FRORIEP; and LOCY and HILL have traced the continuous history of the neuromeres to the time of their merging into the permanent brain vesicles.   The work of these last two authors is evidently most painstaking and their results are so complete and so far in agreement that they may be taken to represent the present state of knowledge of the neuromeres.   They agree in assigning three neuromeres to the fore-brain and two to the mid-brain. The writer may say that at first he was strongly inclined against the conclusions of these authors on account of the unexpectedly large number of segments recognized in the anterior part of the brain.   However, he has lately made some observations on amphibian embryos (*Amblystoma punctatum*), repeating and extending those made by LOCY, and although these observations are not yet complete they seem thus far to confirm LOCY's work.   Further, it will appear in the course of this paper that the point of view from which the subject is approached leads to the acceptance of the number of neuromeres described by LOCY, as necessary to account for all the nerves and sense organs connected with the brain.

NEAL (96, 97) has studied the neural segmentation in selachian embryos and does not accept LOCY's interpretation of the early segments in the fore part of the brain as true neuromeres. He has called especial attention to the existence of a blank neuromere between Nn. V and VII and his description enables

us to determine that this blank neuromere is the one following that which gives rise to the cerebellum, while in higher vertebrates it is the second one behind cerebellum.

5.   *Typical sense organs of vertebrates.*

According to the recent work of DOGIEL (24), Amphioxus possesses sense organs which in structure are comparable to the sense cells of invertebrates on the one hand and on the other to the olfactory organ of craniates.   Sense cells of similar kind have since been described by MARENGHI (88) for Petromyzon. From his own study of the epidermis of Petromyzon the writer is led to think that MARENGHI's interpretation of these elements is more or less doubtful.   The discovery, however, if it should prove correct, is most interesting and important and confirmation of MARENGHI's description is very much to be desired. All other sense organs of craniates are apparently distinct from any found in acraniates or invertebrates ; namely, eye, pineal organs, ear and lateral line organs, and end buds or taste buds. The specialized sense organs found in higher vetebrates need not be considered here.

The literature on the morphology of the sense organs in the skin and mucosae has been reviewed elsewhere (70), with the result of showing that they fall into two categories : the end buds and taste buds belonging to the visceral sensory division, and the neuromast organs (ear, canal and pit organs, ampullae, SAVI's vesicles) belonging to the cutaneous or somatic sensory division.   A reprint of the evidence on which this analysis is based would be out of place here, but as some new facts and discussions of this subject have since appeared it will be of use to print a tabular comparison of all cutaneus organs, their functions and nerve connections.   The table is on an adjoining page (Table A).

The suggestion has been made by ALLIS (4, 5) and COGGI (19, 20, 21) that the ampullae of LORENZINI are homologous with the end buds of teleosts.   Three supports are offered to this hypothesis.   One is based on the assumption that the center for fibers supplying ampullae in selachians is the same as

the center for fibers supplying end buds in teleosts. As has
been pointed out in numerous places (42, 73, 65, 67, 68, 70,
71, 63, 49) this assumption is based merely on the misapplica-
tion of the term "lobus trigemini" by Mayser (90) to the an-

TABLE A. COMPARING CUTANEOUS SENSE ORGANS IN LOWER
VERTEBRATES.

End buds	Neuromasts		
	Pit and canal organs, Ear.	Ampullae, nerve sacs.	Vesicles of Savi.
1. Sense cells slender, rod-shaped, reaching full depth of epidermis.	Sense cells pear-shaped, not reaching full depth of epidermis. Supporting cells rod-shaped.		
MERKEL (91, comparative), MAURER (89, teleosts), HERRICK (48, teleosts), JOHNSTON (68, Petromyzon).			
2. Innervated by communis components. HERRICK (49) and others.	Innervated by various rami of "lateral line nerves." Many authors; see review in (70) and (49).		
3. Fibers slender. STRONG (114), HERRICK (46), and others.	Fibers characteristically thick.		
4. Central endings in lobi facialis (and vagi). HERRICK (47, 48, 49), and others.	Central endings in acusticum, lobus lineae lateralis, cerebellum, and nuc. acust. spinalis. Many authors; see (70) and (49); STRONG (115).		
5. Secondary tract is the secondary vagus tract. Uncrossed (67).	Secondary tract is the tr. bulbo-tectalis, formed by internal arcuate fibers. Crossed. (47, 67, 68).		
6. This tract ends in the secondary vagus nucleus beneath the cerebellum (67).	This tract ends in the tectum opticum (47, 67, 68).		
7. Function is taste; respond only to chemical stimuli. HERRICK (49).	Function of equilibration and hearing.		
	Respond to changes of pressure in surrounding fluid.	Probably the same.	Probably the same.
	Many authors, see (70); PARKER (101, 102).		
8. Distributed in mouth and branchial cavities, and over head, body and fins; in most forms without regular arrangement.	In canals or rows of pits. Regular arrangement in all forms.	Appear in rows related to canals and pits. Sink in, long tubes, collected in groups.	
9. Always superficial.	Always depressed below the surface. (One exception, 48).		Separated from the surface.

terior end of the lobus vagi (lobus facialis or lobus impar). The term ''lobus trigemini'' was commonly applied to the most dorsal portion of the tuberculum acusticum in selachians and ganoids. This lobe was the center for part of the lateral line fibers and has since come to be called appropriately the *lobus lineae lateralis* (65, 49).

In teleosts, where the facial lobe is enormously developed, it overtops the tuberculum acusticum which has no lobus lineae lateralis. MAYSER was misled by the gross anatomy into applying the name ''lobus trigemini'' to the facial lobe. There is no relation, connection, or similarity between the lobus lineae lateralis in selachians and ganoids and the lobus facialis in teleosts to which for a time the same name was erroneously applied. The homologues of both exist side by side in cyclostomes, selachians, and ganoids and their distinctness and dissimilarity can be easily demonstrated.

The second support is that the ampullary pores of the ophthalmic row stand in the same position relative to the supraorbital canal as do the first formed end buds in Amia. The writer is unable to see that the mere position of a cutaneous sense organ is a safe guide to its homology. It certainly can not have much weight in the absence of any evidence from the side of structure, innervation, or function.

Third, ALLIS and COGGI find evidence of homology between end buds and ampullae in the statement made by WIEDERSHEIM and others that all cutaneous sense organs, including end buds, have the same fundamental structure and that the different kinds of organs pass into one another by gradual modifications. The writer has objected (71) that this statement is not borne out by the descriptions of these organs by various workers, but that there is a fundamental difference in their structure as shown in the above table. MAURER (89) has been quoted (5) as witnessing the similarity of structure. I am unable to see that the paragraph quoted (p. 300) offers such evidence. The context shows that *in writing that paragraph* MAURER had in mind only the various forms of acknowledged lateral line organs. In fact the whole paper give one the im-

pression that MAURER is not primarily interested in the homol-
ógy of šense organs. He does not give much attention to end
buds and does not seem to realize the possibility that they may
not be homologous with lateral line organs. He overlooks end
buds in Petromyzon, but clearly distinguishes them from
lateral line organs in teleosts (p. 75-76). Only on p. 148,
in an unexpected connection, do I find an attempt to compare
the structure of end buds and lateral line organs with a view to
showing a genetic connection between them. After referring
to the distinction made by all authors between "birnförmige
Sinnes- und fadenförmige Stützzellen" he cites LEYDIG's belief
that both are sense cells. He then says: "Es ist also sehr
leicht möglich, dass lange Zeit diese beiden Zellformen spezi-
fische Sinnesfunktionen haben. Diese Auffassung wird durch
die Thatsache unterstützt, dass bei Knochenfischen in grosser
Verbreitung Hautsinnesorgane auftreten, welche nur aus einer
Zellform bestehen und diese Zellen gleichen vollkommen den
Stützzellen der höher ausgebildeten Formen." Thus the gene-
tic relation of the two kinds of organs would rest upon the
homology of the *sense cells* of end buds with the *supporting cells*
of lateral line organs. If this is the only way to find a genetic
connection between the two kinds of organs, this fact itself
would seem to offer the strongest evidence against the proposed
homology.

The discussion of the morphological and physiological re-
lationships of the visual and olfactory organs may best be re-
served to a later part of this paper (Secs. 13 and 15).

6. *The anterior end of the head.*

The importance of the question of the anterior end of the
head and brain can scarcely be exaggerated. It is evident that
whether we suppose the anterior end of the brain to be at the
so-called lobus olfactorius impar or in the region of the infun-
dibulum, the number of segments falling between that point
and, let us say, the III nerve would be greatly altered. Also,
a number of important structures which would be ventral in
position according to one view would be dorsal upon the other.

Indeed it may be said that our attitude toward the facts which determine the location of the anterior end of the head largely determines our attitude toward the whole head problem.

The questions of the anterior end of the brain and of the head are inseparably connected. The anterior end of the brain may mean two things according as we consider the axis of the brain cavity or the mid-line of the medullary plate. If the neuropore is the open end of a tube which is equally long dorsally and ventrally, then the anterior end of the axis of the cavity would lie in the same dorso-ventral plane as the anterior end of the mid-line of the medullary plate, and that portion of the tube which forms the border of the neuropore would form a ring every point of which falls equally near the anterior end of the head. As such an assumption begs some of the questions at issue it is inadmissible, and we must take the safer course of considering the primitive brain as a flat plate whose anterior end is marked by the point at which its mid-line passes over into the general ectoderm. It is customary to say that this point is at the lower border of the neuropore. This definition of the anterior end of the brain would be satisfactory if it were shown that the lower border of the neuropore occupies the same position in all vertebrates with reference to other structures of the head and with reference to structures within the brain itself. It is probable that it does not. It is necessary, therefore, to take a wider view and determine the front end of the head as a whole.

The anterior end of the head is marked by *that point at which the brain plate meets the general ectoderm at the same time that it comes into contact with the anterior end of the entoderm in those vertebrates in which the praeoral entoderm is most completely preserved.* This definition does not indicate in advance any particular point that must be accepted as the anterior end of the head. There is in every vertebrate embryo a common point at which brain, ectoderm and entoderm meet. It is a most reasonable assumption that for the given animal such a point marks the anterior end of the head. Following this mode of reasoning KOLTZOFF (76) locates the anterior end of

the brain in Petromyzon in the infundibular region some dis-
tance behind the future chiasma. In some other lower verte-
brates the same reasoning would place it in front of the chiasma.
The difference in the two cases is found in the length of the præ-
oral entoderm. Further, it appears very probable that not all
vertebrates agree in the position of the neuropore and in its
mode of closing. In mammals (36) the lower border of the
neuropore at the time when the eye vesicles are forming lies at
a point which in the adult is behind the chiasma on the topo-
graphically ventral wall of the brain. The point in question,
too, meets the entoderm and is met by the hypophysis in proc-
ess of formation. If this be the anterior end of the brain then
the optic vesicle and the olfactory bulb are dorsal organs lying
in succession in the order named caudal to the anterior end of
the brain. Since the lower border of the neuropore in lower
vertebrates is topographically some distance in front of the
chiasma, it is evident that in mammals the chiasma must form
across a closed up portion of the neuropore which is wanting
in the lower forms. Although His did not deal with this ques-
tion, a re-examination of his writings with this point in mind
leads me to think that his observations were in accord with the
statement just made. In his paper on the general morphology
of the brain (53) he defines the anterior end of the brain as fol-
lows: "Diese basilare Axe [die Mittellinie des Hirnbodens] en-
digt unzweifelhaft in der Basilarleiste. Versteht man dagen
unter Gehirnaxe eine Linie, welche der Mitte der Röhrenlichtung
folgt, so wird diese mittlere Axe in einer Ebene liegen,
welche die Grund- und die Flügelplatte des Gehirns von
einander scheidet, und ihr Endpunkt trifft die vordere Endfläche
im Recessus opticus, bez. dicht vor dem Ort des chiasma
opticum. Wollen wir zur basilaren und zur mittleren Axe noch
eine dritte dorsale Längsaxe oder Längslinie annehmen,
so haben wir deren Ende am oberen Rande der Lamina termin-
alis zu suchen, vor der Stelle, wo die Fissura chorioidea ihren
Anfang nimmt." Since the Basilarleiste is situated behind the
optic chiasma it would seem that His referred the ventral
border of the neuropore to a point topographically ventral and

caudal to the chiasma. His also distincly states that the front
end of the entoderm meets the brain at the Basilarleiste and
only in the frog does he figure this part of the entoderm
(SEESEL's sac) as extending forward beyond the Basilarleiste.
Although in discussing a question in which phylogeny is of
such great importance we should probably not consider the con-
ditions in mammals as of primary significance when they differed
from other vertebrates, yet it is obvious that we have reached
no concordant results in various classes of vertebrates with refer-
ence to the criteria thus far applied.

In order to fix the anterior end of the head in primitive
vertebrates it is necessary not only to locate the point of con-
tact of brain, ectoderm and entoderm, but to locate this point
*in those vertebrates in which the praeoral entoderm is most completely
preserved.*

The animals which best meet the requirements of our defi-
nition are the selachians. In these (119, 106, 107, 57, 96, 97,
17) the praeoral entoderm occupies a median position forming
a bridge between the anterior head cavity and somite 1 of the
two sides. It extends forward immediately beneath the brain
until it meets the ectoderm at the point of junction with the
brain plate. Laterally from this point are the ectodermal thick-
enings which constitute the nasal plates. These are connected
across the middle line by a thickened ridge which is continuous
with the border of the neural plate before, and for a short time
after, the rolling up and closure of the neural tube. Just below
this point appears the ectodermal pit which forms the hypophysis.
So far as selachians are concerned, the anterior end of the head
and brain can scarcely be put at any point on the brain wall which
is topographically below or behind this meeting place of entoderm
with brain plate and nasal plates—for all such points are behind
the anterior end of the entoderm. To seek the anterior end of the
brain at any point topographically in front of the lower border
of the neuropore implies that some part of the margin of the
neural plate may be morphologically anterior. Such a view
could be accepted only if it were shown that the neuropore
closed by fusion of its lips from below as well as from above.

I do not know of any evidence that this takes place in selachians. The lower border of the neuropore lies a short distance in front of the optic stalk, a vestige of which persists as the praeoptic recess (recessus opticus) in the adult. The morphologically anterior end of the brain in selachians is therefore slightly in front of the praeoptic recess and probably behind the anterior commissure. Ventral to this point an ectodermal pit forms the hypophysis and lateral to the same point paired ectodermal patches and corresponding expansions of the brain wall adjacent to the neuropore form the nasal epithelia and olfactory bulbs respectively.

The developement in amphibia is exactly similar to that in selachians. In *Amblystoma punctatum* the continuity of the neural plate with slightly thickened ectoderm at the lower border of the neuropore is present, the entoderm sends forward a median solid prolongation in front of the mouth which meets brain and ectoderm at their point of fusion and overlies the slight depression from or in which the hypophysis is later formed. The median mass of praeoral entoderm corresponds in all essentials to the median entoderm in selachians described above. In Necturus, Miss PLATT (108) describes a median mass of mesentoderm in the same position which she homologizes with the median entoderm between the anterior head cavities in selachians. His's figure of the frog embryo which shows the praeoral entoderm in the same relations has already been referred to. The thickened ectoderm forming the anterior limb of the hypophysial depression in Amblystoma is continuous laterally with the nasal epithelium. When the hypophysial invagination takes place it forms a slender pouch which presses upon the ventral side of the praeoral entoderm slightly behind its tip. All the relations are as in selachians except that the anterior head cavities are not formed and the praeoral entoderm is much shorter. Since the relations just described are most clearly seen at the time when the neuropore is closed and later, there can be no question of the closing of the neuropore from below upwards. Hence the point at which the lower border of the neuropore meets the praeoral entoderm must be taken as the anterior end

of the head in Amblystoma. The relations described are fully maintained until after the optic vesicle and stock are well formed; indeed, the invagination of the hypophysis does not begin until this time. It is therefore easy to determine that the anterior end of the brain lies in front of the optic groove, that is, just in front of the praeoptic recess of the adult. Immediately in front of this is formed the anterior commissure, and above this is the lobus olfactorius impar which marks the dorsal border of the neuropore.

It may be necessary to add that when I say just in front of the optic groove I mean to indicate an appreciable distance, a sufficient distance to have morphological value. If I were to attempt to fix very accurately the point in question in Amblystoma I should put it nearer the anterior commissure than to the praeoptic recess. Thus it will be seen that while my result is closely related to that of His, there is a distinct difference which, as later pages will show, is of considerable importance for segmentation. It should be said, however, that the data on which His based his conclusion would not exclude the result at which I have arrived in the study of amphibia.

Before accepting this result as final, it is necessary to compare lower and higher forms. It seems certain that in the matter of the cephalic extent of the entoderm and mesoderm the selachians are the most primitive vertebrates. In the matter of the branchial apparatus and hypophysis, however, the cyclostomes present more primitive conditions. These conditions are very well known from the work of DOHRN (25), KUPFFER (78) and KOLTZOFF (76). The hypophysis reaches a much greater developement than in other vertebrates and in Bdellostoma (KUPFFER) communicates openly with the archenteron before the definitive mouth opening is formed. In the front wall of the hypophysial pit are formed at first a median and afterward paired lateral ectodermal thickenings which later form the nasal epithelium. The hypophysis fuses with the foremost end of the entoderm and this comes into contact with the brain at the infundibular region (KOLTZOFF). Here we have relations similar to those in selachians but with important differ-

ences: the entoderm does not extend far in front of the noto-
chord or mouth but meets the hypophysial ectoderm at a point
relatively far back along the lower wall of the brain. To harm-
onize the facts in cyclostomes and selachians it is necessary to
suppose that in the cyclostomes the hypophysis has pushed
back further than in selachians while the entoderm and
mesoderm have been less well developed, and the point
of meeting falls beneath the infundibulum instead of at
the lower border of the neuropore. The criticism might
be made on this that the writer has arbitrarily chosen
the selachians, in which the entoderm is well developed,
in preference to the cyclostomes in which the ancient
stomodaeum is better developed. That the choice is not arbi-
trary, however, is clear from two facts. First, not only is there
actually a longer praeoral entoderm in selachians, but there are
definite paired lateral structures developed (the anterior head
cavities) which certainly have some segmental value whether
they be considered as somites, lateral plate mesoblast, or aborted
gill pouches. Second, the same region of the brain is related
to the olfactory placode as in selachians and amphibia. There
has actually been a greater reduction of entoderm and meso-
derm in cyclostomes and the brain projects farther forward in
relation to them. The hypophysis, however, in the absence of
the entoderm is able to become deeper. The writer is therefore
forced to the conclusion that the selachians and amphibia indi-
cate more reliably than the cyclostomes the anterior end of the
head and brain. If we fix the anterior end of the brain in
cyclostomes, in harmony with the selachians, at the point of con-
tact of the nasal pit with the brain wall it would be, according to
the figures of KUPFFER and KOLTZOFF, about midway between
the praeoptic recess and the "lobus olfactorius impar," or very
near to the anterior commissure. So also the figures of DOHRN
(25) and HIS (53).

Since finishing the manuscript it occurs to the writer that
the above account might be taken to imply that the entoderm
extends into the region which later in the paper is called the
prostomium. Such of course is not the intention. The pro-

stomial area is extremely short in the early embryo and in fact assumes appreciable size and definite form only after the period at which the relations between the brain plate, ectoderm and entoderm above dealt with are in evidence. The term ''anterior end of the head'' as used here really applies to the base of the prostomium, or the most anterior point to which the two primary germ layers extend. The anterior tip of the prostomium consists of ectoderm alone and could be located only by reference to the point determined upon as the result of the above examination.

7. *The segment containing N. III. Segment 5.*

Neuromere **v**, somite 1, N. profundus, N. III.

To fully describe a given segment it is necessary to determine what representatives are present of the skin, dorsal mesoderm, lateral mesoderm, and gut, and of the somatic sensory, somatic motor, splanchnic motor and splanchanic sensory divisions of the nervous system severally related to these structures. If any of these components of a true segment are absent their absence should be accounted for, and a functional relation between the nerves recognized and the segmental organs present should be clearly shown.

In determining the neuromere to which a somatic motor nerve belongs it should be remembered that these nerves emerge from the brain as ventral roots in the constrictions between the neuromeres. Since a neuromere is considered to be the convex segment between two constrictions, it is most convenient to assign the ventral roots to either the preceding or the following neuromere. In the trunk region where in all higher vertebrates the dorsal and ventral roots unite in the spinal ganglia the ventral root should be assigned to the neuromere with which the dorsal root is connected. The relative position of the dorsal and ventral roots, the neuromeres, and the myotomes will be discussed in a later section (Sec. 19); here the result of that discussion will be anticipated and the ventral roots assigned to neuromeres next caudal to the place of origin of the roots.

The somite which gives rise to the muscles innervated by
N. III is universally agreed to be somite 1 (praemandibular) of
v. WIJHE.

The third nerve arises from the ventral wall of the mid-
brain, in some forms far forward toward the point at which the
floor of the brain bends down into the inferior lobes. The
nucleus of N. III is well forward in the base of the mid-brain
and that of N. IV follows not far caudal to it. These relations
in the adult would seem to show that the third nerve belongs
to the first of the two mesencephalic neuromeres, to which,
indeed, some authors have referred it. On this assumption
the IV nerve would naturally be assigned to the second
mesencephalic neuromere. The trochlearis, however, supplies
the mandibular somite (somite 2) and the sensory nerve of this
segment is the trigeminus. The trigminus can not on any
ground be placed farther forward than the cerebellar neuromere.
If, then, Nn. IV and V be assigned to the cerebellar neuromere,
N. III would belong to the second mesencephalic or fifth
neuromere of Locy. To account for the position of the nucleus
and root somewhat farther forward in the adult we have to con-
sider that the nucleus lies at the anterior border of the large
ventral commissure of the cord and brain, which here in the
base of the mid-brain reaches its greatest size and importance
and is known as the ansulate commissure. This great commis-
sural system is composed fundamentally of the decussating
fibers from "tract cells." It has added to it in the base of the
cerebellum and mesencephalon many internal arcuate fibres from
the cutaneous centers, descending tracts from the tectum opticum
to the oblongata and the inferior lobes, the decussation and end
nucleus of the bundles of MEYNERT, and other fibers. Most of
these fiber tracts have developed at a period later than the
formation of the infundibular depression which sets a cephalic
limit to the commissure. The development of these voluminous
tracts has crowded the nuclei and roots of Nn. III and IV for-
ward. Not only the mere crowding due to the size of the
bundles but also the fact that the fiber tracts are related to brain
centers situated farther cephalad, has contributed to this result.

The sensory nerve of this segment is the ophthalmicus profundus. In selachians (119, 124, 58, 59, 96, 97) the neural crest which gives rise to the profundus and trigeminus extends over the mid-brain and cerebellum. As the ganglionic anlages are being formed, those of the profundus and trigeminus are separate, the profundus anlage being connected with the dorsal wall of the mesencephalon and the trigeminus anlage with the cerebellum. At a later time the profundus ganglion has lost its connection with the mesencephalon and its root fibers pass into the brain with the root of the trigeminus. When the profundus and trigeminus trunks are formed the profundus runs forward along the inner side of somite 2 and the outer side of somite 1, the trigeminus runs over the outer side of somite 2. The profundus and trigeminus are therefore one segment apart and belong respectively to neuromeres v and vi.

Essentially the same mode of development is seen in Petromyzon (79, 76), and KOLTZOFF states that the segmental arrangement is the same as in selachians.

The separation of the profundus from the trigeminus as a distinct segmental nerve is of course not new; it is in agreement with the opinion long held by v. WIJHE, WIEDERSHEIM FÜRBRINGER and other comparative anatomists.

The profundus is the general cutaneous nerve of the segment to which somite 1 belongs. Its distribuion to the dorsal surface of the head and snout, above and in front of the eye, seems to indicate that it is only a dorsal ramus and also that in spreading over the snout it has annexed an innervation territory not primitively belonging to it. For the bearings of the latter point see the treatment of segments anterior to segment 5, below. When the head flexure is considered it is seen that the area of distribution of the profundus is dorsal; and the almost total absence of ventral structures in front of the mouth, i. e. between the innervation territory of the maxillaris and the eye and olfactory organ, explains the absence of a ventral ramus. The N. ophthalmicus profundus is therefore to be considered as the sole representative of the general cutaneous component in segment 5, to which neuromere v, somite 1, and N. III belong.

It is either a dorsal ramus alone or has incorporated in it whatever vestige of a ventral ramus exists.

The visceral elements which should be found in a typical head segment are absent from this one. The visceral apparatus is represented in the most primitive forms by very much reduced and transient structures (see sections on the mesoderm and on the anterior end of the head, above), and the splanchnic sensory and motor nerves with their appropiate central nuclei are wholly unknown in this segment.

In the central nervous system, as has been shown elsewhere (69, 70), the caudal part of the tectum opticum and the nucleus of N. III represent respectively the somatic sensory and the somatic motor divisions of this segment. A further treatment of the sensory center will be found below in the sections on the lateral line system and on the visual organs (Secs. 10, 13).

8. Segment 6.

Neuromere **vi**, N. V, N. IV, Somite 2, mandibular arch, sympathetic ganglion.

In the last section reference has been made to the structures found in this segment, and part of the evidence for their relations given. For the bringing together of Nn. IV and V in one segment we have a long line of investigations including v. WIJHE (119), HOFFMANN (58, 59), PLATT (106), NEAL (76, 97), and KOLTZOFF (76). For the relations of somite 2 and the mandibular arch respectively to these two nerves abundant evidence is found in the same papers. It must be noticed that N. V contains both general cutaneous components for the skin of this segment and viscero-motor fibers for the muscles of the mandibular arch. These muscles are formed from the lateral mesoderm and the nucleus of origin of the motor V belongs to the lateral motor column in the oblongata (70). There are found, then, all the elements of a typical segment except the splanchnic sensory nerve component and its center. The only vestige of this component found in any vertebrate is the sympathetic ganglion which will be treated below in the general section on the sympathetic. The small entodermal area belonging to this segment, if indeed there is any, is supplied by com-

munis components in the palatine branch of the seventh nerve, and there is accordingly no communis component in the trigeminus and no viscero-sensory center in this segment. In the exceptional case of Amia (3) a large number of communis fibers enter the trigeminus from the facialis root, to be distributed to end buds on the surface of the head. Even here the communis fibers do not belong to the trigeminus segment.

The central nervous structures related to the nerves of this segment include the cerebellum and the nuclei of the spinal V tract, the motor nucleus of N. V which lies a short distance in front of the nucleus of N. VII in the oblongata, and the nucleus of N. IV which lies in the base of the mid-brain. From the adult relations of centers and nerve roots it would be difficult to decide with what neuromere they are associated. This is especially noticeable when attention is called to the fact that the root of N. V is connected with the cerebellar segment in some forms, while in others it is distinctly further caudad. If we look to embryology to determine its primitive location we find the same difference in different classes of vertebrates. Considering the cerebellar segment as LOCY's neuromere vi, the trigeminus root is found to have the following location. In both the embryo (76) and the adult (68) of Petromyzon it is connected with neuromere vi. In selachians (124, 106, 58, 96, Fig. 6, 97) it is connected with neuromere vi, in the embryo and shifts to neuromere vii. The actual shifting has been seen and clearly described by ZIMMERMANN. It appears also in NEAL's (97) figures 15 to 21. In teleosts(52) it has the same relations. In a Salmo embryo of 23 days it is connected with the cerebellar neuromere; at 31 days it has shifted to the neuromere following. In amphibia (118) it is connected with neuromere vi in the embryo. In the lizard (56, 99, 87), chick (52) and pig (92) the trigeminus is connected with neuromere vii in the embryo. GIGLIO-TOS (40) describes a shifting of the ophthalmic and trigeminal roots in the human embryo from the mesencephalon to the hind-brain. From this series it must be thought that there has been a shifting backward of the trigeminus during the phylogenetic history of vertebrates. The reason for this shifting is probably to be found

in the place of ending of the cutaneous fibers within the brain, although shifting of other structures (to be spoken of below) may have aided or at least offered favorable conditions. In Petromyzon (68) a part of these fibers go directly to the cerebellum, others bifurcate and send one branch to the cerebellum and the other backward, and the remainder turn directly backward to end in the acusticum or the nucleus funiculi. In selachians (63, 28) and in ganoids (67) the destination of the fibers is practically the same. In amphibia (123) a part of the trigeminus fibers enter the cerebellum. In higher vertebrates few if any sensory V fibers go to the cerebellum; they run regularly to the nuclei funiculi. Here, then, is a shifting of the place of central ending of these fibers corresponding to the shifting of the root. The writer would interpret these facts as follows. The general cutaneous fibers of the trigeminus, as of the spinal nerves, typically bifurcated on entering the brain; in primitive vertebrates the ascending fibers ended in the cerebellum or farther forward, the descending fibers passed backward varying distances. The reduction of general cutaneous area in the region of the IX and X nerves due the disappearance of postauditory myotomes, and the developement of the lateral line system resulted in the general cutaneous centers in the cerebellum and oblongata coming gradually into the service of the special cutaneous sense organs (neuromasts and ear). Concurrent with this was the specialization of the cerebellum as a center of coordination. These processes account for the gradual shifting of the general cutaneous fibers of the trigeminus which we observe in vertebrates, until they are all collected in the spinal V tract leading to the nuclei funiculi at the caudal end of the oblongata. Along with these processes, then, and probably as a result of them, we find the root of the nerve shifting back one segment nearer the place of ending of the fibers. The shifting of the whole root of the profundus from the mesencephalon to join the trigeminus is a more conspicuous example of the same process carried out earlier. Both of these shiftings are repeated in the ontogeny in lower vertebrates, as we have seen. On the ground of the source of the V ganglion and the position of its root in

the more primitive forms, and the place of ending of its ascending fibers in fishes and amphibia the writer has assigned N. V to the cerebellar neuromere, **vi.**

In connection with the ganglia of the profundus and trigeminus are dorsal-lateral placodes giving rise to cells whose fibers form the Rr. ophthalmicus superficialis and buccalis of the facialis. These are of great importance for the interpretation of the lateral line components and their relation to the general cutaneous system. They will be referred to again (Sec. 10).

The exit of the trochlearis from the dorsal surface of the brain and its decussating at that point is a puzzle for which no adequate solution has yet been offered. The writer has only a brief suggestion to make. The course of the root fibers dorsally through the brain wall may be due to the course of the fiber tracts among which they run. The position of the nucleus of the nerve relative to the tracts which form the ansulate commissure in typical fishes suggests strongly that the axones from the cells of the trochlearis nucleus may have followed some of these bundles as the path of least resistance. The tracts between the tectum opticum and the base of the oblongata, the tracts between the inferior lobes and the cerebellum, and others, all running more or less dorso-ventrally in the side wall of the brain and decussating ventrally at the level of the trochlearis nucleus—these bundles, which lie ectal to the nucleus of the trochlearis, may have constituted an effective barrier to the axones of the trochlearis in their attempt to reach the ventro-lateral surface of the brain. The axones may then have turned upward along the ental surface of these bundles until they reached the dorsal surface of the brain. If the fibers were thus directed in their course they would be carried to the mid-dorsal line before gaining an exit from the brain and if they then grew straight on they would pass to the opposite side. In Acipenser (67, p. 139) the root fibers are so intimately wrapped up in a heavily medullated bundle which rises from the region of the nucleus of IV to the dorsal surface of the cerebellum that it is easy to imagine the course of the root being determined by the

cause just mentioned. It is a serious question, however, whether this influence would have been sufficient to determine the course of the root in more primitive forms where the tracts in question are less highly developed. In Petromyzon, although the tracts between the inferior lobes and the cerebellum are very small, the ascending and descending tracts between the tectum and the oblongata are relatively larger and more conspicuous than in Acipenser. There is good reason for thinking that these tracts are among the most primitive and fundamental in the brain, so that their influence would be felt in the lowest forms. It should also be noticed that on account of the late appearance of the trochlearis we may suppose that these sensory tracts may have been already laid down before the fibers of the nerve grew out.

It may be mentioned here that the ventral decussation of a part of the fibers of the third nerve may have been brought about in a similar way. The nucleus of III lies among the bundles of the ansulate commissure and in Petromyzon, where the decussation of the nerve is large and conspicuous, the position of its fibers (68, Fig. 24) suggests that their course may have been determined by the path of least resistance offered by fiber tracts already laid down.

9. *The absence of nerve roots from one or more hind brain segments and the determination of the neuromere concerned.*

The only reference which I have seen made to the blank neuromere (Sec. 4 above) as having special segmental significance is by NEAL (96, 97) who uses it in support of the hypothesis that one branchial segment has been supressed, the hyoid arch representing two arches and this neuromere being deprived of nerve roots in consequence. This hypothesis was first brought forward by van WIJHE and has been supported by Miss PLATT (106) and HOFFMANN (127). KOLTZOFF (76) strongly argues that there is no ground in the development of the mesoderm and the gills for the supposition that a branchial segment has been suppressed. The writer is unable to see the advantage of the hypothesis of a lost gill. No reason or cause has

been given for the disappearance of a gill in the middle of the series. The only indication of it is the connection of somites 3 and 4 with the hyoid arch in selachians. This would indicate that the lost gill slit must have cleft the present hyoid arch, as v. WIJHE thought. Since it is impossible to explain the nerve relations on this supposition, NEAL (96) suggests that the lost branchial segment must have been "anterior to the present hyomandibular cleft," corresponding in position to the blank neuromere between Nn. V and VII. Even so, the praetrematic and posttrematic rami of VII are made to embrace two gills, the present hyomandibular cleft and the lost one; unless, indeed, it is supposed that the lost cleft divided the mandibular arch between the mandibularis V and the mandibularis VII nerves. On the ground of mesoderm, however, it is the hyoid that is supposed to have been cleft. BRAUS' Figs. 5 and 6, Pl. XXI, indicate that the connection of somite 4 with the hyoid arch is secondary. One very important feature of this blank neuro-mere which has not been noticed by previous authors is that it is not the same in all vertebrates, but shifts caudad in higher forms just as the trigeminus does. This does not seem to have any relation to a lost gill in the hyoid region. Since the hy-pothesis of a lost gill was brought forward to explain the nerve relations, it loses its interest if these relations are satisfactorily explained on some other basis.

For the explanation of the blank neuromeres the most sug-gestive facts are found in the position of the auditory vesicle and in the position of the nerve centers related to the cranial nerves. In Petromyzon (KOLTZOFF'S figures), the auditory vesicle when first formed lies oposite neuromere vii and the facial ganglion passes down mesial to its caudal portion. In the adult (1, 68) N. VII passes through the mesial wall of the audi-tory capsule and out through the ventro-cephalic angle. There has apparently been some shifting back of the auditory sac dur-ing the ontogeny of Petromyzon. In selachians and all Gna-thostomes the auditory sac is situated farther back, about opposite the tenth or eleventh neuromeres. During the early development in *Squalus acanthias* (125) the auditory pit

shifts back from neuromere ix to neuromere xi. Such an amount
of shifting of the relative position of the auditory vesicle
and brain can scarcely have failed to influence the segmental
position of the nerve roots. HILL's figures (52) also show a
slight shifting of the auditory vesicle during development in
teleosts. The relative position of the auditory vesicle and the
nerve roots also changes, as indicated in part above. From
lying opposite a blank neuromere between Nn. V and VII in
the embryo of Petromyzon, in the lower Gnathostomes it
comes to lie between the roots of Nn. VII and IX which are
crowded apart by the vesicle although they remain connected
with successive neuromeres. In reptiles, birds and mammals the
vesicle is found between Nn. VII and IX and there is a blank
neuromere opposite it, in addition to the blank between Nn. V
and VII. It is a noteworthy fact that in mammalian embryos
the VII-VIII ganglionic complex lies wholly in front of the
vesicle, while in lower vertebrates it lies between the vesicle and
brain.

If we couple with this shifting of the auditory vesicle a
tendency to concentration of the centers for the V, VII and X
nerves, I think we shall find sufficient cause for the observed
arrangement of the nerve roots. The visceral sensory fibers
form a descending tract (*fasciculus communis, f. solitarius* in man)
and end in relation to cells accompanying the tract and in the
nucleus commissuralis at the caudal end of the oblongata. The
general cutaneous fibers run caudally in the spinal V tract. The
motor roots are formed by fibers which arise from nuclei caudal
to the place of exit of the roots and run forward parallel with
the somatic motor fasciculus. Under these conditions it is
reasonable to suppose that there may have been a shifting back-
ward of the nerve roots toward their centers. The efficiency
of this influence seems especially clear in the case of the com-
munis components, many of which primitively decussated in
the dorsal commissure of the oblongata (Sec. 17). As the
formation of the choroid plexus crowded this commissure back-
ward to the present position of the commissura infima Halleri,

the root fibers would certainly be influenced to shift backward with it.

The history of events which have led to the appearance of blank neuromeres in the oblongata, then, is thought to be as follows. The auditory vesicle attained a size in cyclostomes sufficient to push apart Nn. V and VII between which it was situated. Later in the phylogeny there was a migration of the auditory vesicle backward, which was possibly connected with the reduction of myotome 4 and following. This migration, together with a process of concentration of the nerve centers, resulted in carrying all the nerves in question back one segment; Nn. profundus and V following the shifting vesicle for the advantage of approaching their centers, and Nn. VII, IX and X crowded back by the vesicle at the same time that they come nearer their center. The movement of the vesicle was more rapid than that of the roots and the vesicle came to lie between Nn. VII-VIII and IX. Finally, after this position had been assumed, the further expansion of the vesicle crowded N. IX farther back and caused a blank neuromere at this point in reptiles, birds and mammals.

The shifting from the primitive condition which we have supposed may be summarized thus:

Petromyzon: V not shifted; VII and IX shifted one neuromere, crowding upon X.

Lower gnathostomes: V shifted one, VII, IX and X shifted two neuromeres.

Reptiles, birds and mammals: V shifted one, VII shifted two, IX and X shifted three neuromeres.

We may suppose that there was first, in the lower vertebrates a crowding together of IX and X and then a shifting back of both into those neuromeres whose branchial nerves have been collected by N. X (see Sec. 12).

The blank neuromere was originally the one following the cerebellum and the elements composing the head segment to which this neuromere belonged were: Neuromere vii, somite 3, hyoid arch, somatic motor N. VI, splanchnic motor N. VII, splanchnic sensory N. VII, and a general cutaneous component

of N. VII which is unknown. (But see 73). The position of N. VI and the absence of a general cutaneous component have not yet been accounted for. N. VI innervates the muscles derived from somite 3 and its nucleus of origin and root are found at approximately the same level with N. VII in all vertebrates except Petromyzon. Whether its usual position is to be accounted for by supposing that it has shifted back at the same time with the other nerves, or by supposing that it represents the ventral nerves of two segments requires further investigation. I am inclined to think that NEAL's reasoning is right in this matter and that the latter is the more probable interpretation. However, no support for this was found by KOLTZOFF in the development of Petromyzon where we should have most expected it. The writer is convinced that the adult relations of N. VI in Petromyzon are not correctly described and he hopes soon to re-investigate them.

For the explanation of the absence of a general cutaneous component from this segment, also, we must await further investigation. Such a root should be present for the innervation of the skin around and above the hyomandibular cleft in cyclostomes and selachians, and in operculated forms for the innervation of the operculum. The hypothesis may be suggested that in the process of shifting above described the general cutaneous fibers which originally accompanied N. VII remained in neuromere vii and were absorbed by N. V, so that the general cutaneous fibers of three segments are concentrated at the profundus-trigeminus root. The fact that a part of the operculum in teleosts (46) is innervated by the trigeminus is consistent with this hypothesis. If the corresponding area in cyclostomes and selachians should have the same innervation, it would give strong support to the suggestion just made.

10.   Segment 7.   The acustico-lateral system.

In the primitive condition this segment was probably composed of the following elements: neuromere vii, somite 3, hyoid arch, somatic motor N. VI, splanchnic motor N. VII, general cutaneous component (?), and splanchnic sensory N. VII, with the

appropriate centers. In cyclostomes neuromere vii is blank and neuromere viii is related to the structures enumerated. In gnathostomes neuromere viii is blank and neuromere ix is related to the same structures—not that neuromere viii in cyclostomes or ix in gnathostomes lies in the same transverse plane as the other structures of segment 7, but that it is connected with those structures by the nerve roots. In Fig. 10 the relations are shown as in Petromyzon; in Table B the same facts are presented by giving to each element its hypothetical primitive position and stating the shifting which is supposed to have taken place.

In all craniata the neuromasts with their fiber components and centers are added to the above structures. These now require some attention.

The essential unity of the acustico-lateral system both peripherally and centrally and the close relation of these organs and centers to the general cutaneous system is assumed (67, 68, 70). It is a natural inference that the neuromast system has been derived from the general cutaneous. Further, it has been shown by the work of numerous authors that the whole neuromast system grows peripherally from *the vicinity of* the auditory pit as a starting point, that the fibers enter the brain at a common point near the auditory nerve, and that the same sensory nuclei serve as the centers for all these fibers. It therefore seems pretty clear that we may look for the origin of the neuromast system as a modification of the general cutaneous system of a given segment or small number of contiguous segments, and that the center of the neuromast system was primitively in about the region of neuromere vii, opposite which the auditory pit now makes its appearance in the lowest known vertebrates.

Although the neuromast nerves have usually been regarded as dorsal rami (when they have not been given the dignity of complete dorsal roots) a difficulty arises in the fact that the ganglion cells of the neuromast rami are derived from ecodermal thickenings, and that the placodes of nerves for the head lines are at first in connection with such undoubted dorsal rami as the ophthalmicus profundus and ophthalmicus superficialis trigemini.

The origin of the nerves from ectodermal placodes has led to the development of the hypothesis of primary and secondary sense organs, to which the HERTWIGS, RETZIUS, v. KUPFFER and others have contributed. The hypothesis may be stated as follows. The dorsal-lateral placodes in the vertebrate embryo represent a series of primary sense organs in which the sensory cells were of a type illustrated by the cells of the olfactory organ in vertebrates or by the usual sense cells of invertebrates. Such sense cells send their own axones into the central nervous system. There has been a gradual sinking of these sense cells beneath the surface comparable to the migrating inward of sensory epithelial cells in invertebrates. The sinking in of cells from the primary sense organs is repeated in the ontogeny and the cells become the ganglion cells of the lateral line nerves. Then there appear in the placodes newly differentiated sense cells, the neuromast or pear cells characteristic of lateral line organs which constitute secondary sense organs.

It should be noticed with regard to this account of the lateral line organs and nerves, first that there is no direct evidence for this interpretation of the placode cells; and second that it does not imply any close connection between this system and the general cutaneous system. Also, it seems to the writer that a somewhat more simple explanation of the origin and relationship of the neuromast system may be found. The above hypothesis postulates the existence primarily of the sense organs of the invertebrate type, the transformation of these into ganglia, and the new formation of sense organs of the neuromast type. While the transformation of sense cells into ganglion cells is not unthinkable, yet the transformation of a cell possessing a specialized sensory peripheral process into one whose peripheral process is adapted to receive stimuli from another cell with which it enters into complex relations is a very profound change. Moreover, what advantage is gained by the replacing of primary sense cells by secondary sense cells and the addition of one link to the sensory chain is difficult to see. Any change which increases the length of, and the number of relay stations in, a reflex arc would generally be considered to be disadvantageous.

Finally, the process by which the primary sense cells are supposed to be transformed into ganglion cells is compared to the process in lower invertebrates by which the epithelio-sense cells wander inward to help form the central nervous system.   While this again is conceivable it should be noticed that it is quite the opposite to what we see going on in the vertebrates ; namely, the wandering of cells *out* from the central nervous system toward the areas of their distribution.

The writer would suggest that the facts may be equally well explained by supposing that the placodes represent material comparable to the neural crest which has separated more completely from the brain tube than has the remainder of the crest, and that the new formation of neuromast cells is the only peculiar feature of the acustico-lateral system.   It is not certainly known what nerve components owe their origin to the neural crest but the writer believes that the general cutaneous component is universally regarded as having that origin and the same assumption is at least tacitly made for the general visceral component.   It seems probable from our present knowledge that ; (1) in Amphioxus all or the greater part of the material representing the neural crest of vertebrates is included within the brain tube; (2) in selachians, teleosts, and amphibia at least, a part of the cells whose dendrites supply the skin and which are homologous with the general cutaneous ganglion cells remain within the spinal cord during embryonic and in some cases adult life ; and (3) the neural crest presents all degrees of separation from the neural tube during the development of the embryo. In some selachians (59) it separates from the neural tube by a process of hollow budding, while portions of some of the ganglia are formed of cells which migrate out from the lateral surface of the brain at a comparatively late period.   In amphibia the relations of the neural crest vary greatly, but in Necturus (108) there is an unusually close connection between the brain and the ectoderm through the neural crest and in the case of the VII ganglion cells cells continue for a long time to migrate from the wall to the ganglion, while the V ganglion is very largely formed by cells coming from the ectoderm.   The fact is that there is a

very great variation in the relation of the neural crest to the brain and to the ectoderm. The suggestion presents itself that there has been a progressive separation of the material for the ganglia from the brain and, if the acustico-lateral ganglia be included, it appears that the more highly specialized components came off first, the less specialized last.

The neural crest is to be regarded as fundamentally a part of the central nervous system. This is evidenced by the presence of its equivalent within the nerve cord in Amphioxus, by the fact that it is more or less completely included in the neural tube in craniata when the tube first rolls up, and by the fact that a part of its cells remain within the spinal cord in fishes (38, 39, 66). If this view of the neural crest be accepted, is the neuromast system to be considered as a new structure of peripheral origin, or is it to be brought into relation with other structures represented in the neural crest? The view that it is of peripheral origin gives no explanation of its very intimate connections with the centers of the general cutaneous system in the medulla oblongata and cerebellum. The neuromast system must be supposed to have come into relation with the general cutaneous centers by accident and then to have largely usurped them. Even the suggestion made by KOLTZOFF (76, p. 502) that the general cutaneous ganglia represent an earlier category of primary sense organs which have been transformed into ganglia does not help in this matter. Yet the relation of the neuromast and general cutaneous components in their nerve centers is of so fundamental a character that the writer is convinced that it must be reckoned with as one of the most important factors in the interpretation of the acustico-lateral system.

Two structures, both of which are primitive and transient, and both of which point to the ancestral structure of the nervous system, are significant for the explanation of the origin and relationships of the acustico-lateral system: first, the neural plate stage in the ontogeny of the central nervous system, and second, the existence in the spinal cord of fishes of cells whose dendrites are distributed to the skin and whose neurites behave

as do those of the general cutaneous ganglion cells. The first indicates that the nervous system was in primitive vertebrates a specialized area of the superficial ectoderm. The second fact indicates that the primitive form of cutaneous innervation was by means of dendrites of cells in this specialized area growing out to the rest of the ectoderm. This general cutaneous innervation corresponds to the free nerve endings in invertebrates which come from cells in the central nervous system. That this is the primitive form of innervation for tactile and pressure stimuli in vertebrates, I have no doubt. The peripherally situated tactile cells (hair cells) of the highly specialized arthropods do not appear to me to be in the line of vertebrate development. Granted that the sensory cells which supply free nerve endings to the ectoderm in worms may (or must) once have been derived from the ectoderm, we must nevertheless believe that since these cells gained their position in the central nervous system in the worms that relation has been maintained in the line of vertebrate development. Now the relation of the neuromast system in present vertebrates to the general cutaneous system compels us to seek the origin of the neuromast system as a modification of that already established cutaneous system. This seems the more necessary on account of the phylogenetically late appearance of the neuromast system.

If the line of reasoning thus far is good, we have to make only two suppositions for the explanation of the chief relationships of the acustico-lateral system. First, the area from which the system has been developed originally belonged to the neural plate area ; Second, there have appeared in this area a special type of sense cells characteristic of the neuromast organs. It is not hard to conceive that the neuromast area once formed the marginal portion of the specialized ectoderm which constituted the central nervous system. The idea that the neural crest and neuromast area together formed a marginal band along the primitive neural plate is supported by the position of the neuromast area just behind the broad cephalic plate and by the fact that opposite this area there is a long space in which the neural crest contains no cutaneous elements and in which it is partially

or completely interrupted at two points. We may imagine, then, that when the neural plate rolled up and sank beneath the surface, the neuromast area was left outside ; and we may find the cause for its failure to be included, as the rest of the neural crest was, in the fact that the special sense cells were already developed in this area. If now we consider that the primitive cutaneous sense cells remained in the neuromast area, as their absence from the neural crest of this region indicates, we have all the essential relations of the neuromast organs accounted for. The further development consisted in the sinking in of the area to form a pit for the better protection of the sense cells, or for their better functioning, or both, and the migration of the ganglion cells into the space between the infolded neural tube and the auditory pit, where they found more room. The depressed area became the forerunner of the auditory vesicle and the head and trunk lines of neuromast organs. The general cutaneous sensory cells of the area acquired permanent relations with the newly formed sense cells, and their migration inward to form the ganglia of the lateral line nerves has become a permanent feature of vertebrate development.

The extent of the neuromast area has thus far been indicated only in the most general way for the double reason that we should not expect it to be sharply circumscribed at least in the beginning, and that there are reasons for thinking that it extended farther forward than is generally supposed. The whole of the acustico-lateral system is described as arising in some selachians (93, 125) and teleosts (121, 122) from a single somewhat extensive thickening of ectoderm from which the two head lines grow forward and the trunk lines grow backward. In cyclostomes (79, 76), however, there are two large and separate placodes, in front of the acustico-facialis placode, with which the profundus and trigeminal ganglia come into contact. One would think from the relations that these two placodes, which give rise to the ophthalmicus superficialis facialis and buccalis nerves, belonged originally to the profundus and trigeminal segments. This idea is strengthened by the fact that in the Gymnophiona (11) a placode appears in the same situation

which invaginates and forms a vesicle in all essential respects
like the auditory vesicle.   This is then converted into a gangli-
on which comes into close relation with the maxillo-mandibular
ganglion and gives rise to the ophthàlmic nerve.   A comparison
of this account with Coghill's (22) account of the profundus
and trigeminus nerves in Amblystoma indicates that the nerve
in this case is the ophthalmicus superficialis facialis, and the
placode is the homologue of that which gives rise to the R.
ophth. sup. VII in cyclostomes, some selachians, and ganoids.
That the ganoids are probably to be included here is indicated
by the fact that the continuity of the head lines with the audi-
tory placode has not been found in Amia (6).   From these
facts the writer thinks it probable that (1) the acustico-lateral
system was not originally confined to a single segment; (2) that
it extended forward one or two segments in front of the site of
the auditory pit; (3) that it was largest, however, in that seg-
ment in which the auditory sac was afterward formed, and that
in the other segments it appropriated a greater or less part of
the neural crest material.

Two further questions may now be considered: that of the
segmental relations of the system, and that of its relation to the
general cutaneous nerves.   We have come in late years, and
rightly so, to deny segmental value to the adult lateral line sys-
tem; but here is evidence that primarily it may have extended
through more than one segment.   The fact that three separate
placodes are formed in the lowest forms, cyclostomes, and in
some other fishes and amphibia, suggests that the whole neuro-
mast area was not fully continuous at the start but that it was
early divided into three parts corresponding to the three seg-
ments which it occupied.   (Compare 125, p. 578).   It seems
probable that the supraorbital line, formed from the placode re-
lated to the profundus; the infraorbital line, formed from a pla-
code related to the trigeminus; and the hyomandibular line,
formed from the auditory placode, represented three segments
of the primitive neuromast system.   The lateral line is to be
thought of as a late outgrowth from the auditory placode.   I
am well aware that this is in opposition to the conclusion which

the writer and many others have reached in recent years that the acustico-lateral system should be referred strictly to the same segment with the facialis. But the reasoning here employed is in perfect harmony with the spirit and method which have led us to that conclusion, and the present result is based on new facts. It should be said that the writer does not accord to the neuromast system any value to segmental study except as a landmark, and that the truth or error of the segmental arrangement suggested here does not in any way affect the validity or the general interpretation of the acustico-lateral system given above.

By the relation of this system to the general cutaneous nerves I mean the question whether it corresponds to one or more dorsal rami, or whether it has used up a larger part of the general cutaneous component. From what goes before it is clear that the neuromast system must be thought to have absorbed a variable part of the general cutaneous component in the segments to which the profundus, trigeminus, and facialis belong. It may even be that the whole of the general cutaneous component in the facialis segment has been absorbed, and that this accounts for its apparent total absence in that segment. It is of course evident that the communis component in the neural crest could not enter into the neuromast system, and so all schemes of segmentation which raise the VIII or any or all of the lateral line nerves to the dignity of complete segmental sensory roots are faulty.

11. Segments 8 and following.

The processes which have led to the conditions in the caudal part of the head are discussed in the following section. It will be unnecessary to describe in detail each segment and the changes which take place in each. Figure 10 and Table B show the component parts of these segments in lower vertebrates more clearly than a description in the text could make it. For the facts in the higher vertebrates I can do no better than refer the reader to the extensive descriptions and tabular statements of FÜRBRINGER. These must be read, however, it seems to me,

in the light of the general considerations contained in the follow-
ing section.

*12. The occipital region and the posterior limit of the head.
The constitution of the vagus. Shifting of organs.*

In the occipital region of the head we find the following
peculiar condition. (1) A number of myotomes (beginning
with somite 10 in Petromyzon, somite 9 or 8 in selachians) im-
mediately behind the gills send ventral buds downward behind
and then forward beneath the gill sacs to form hypobranchial
muscles. These myotomes and their ventral derivatives are
supplied by a series of ventral nerve roots from the medulla
oblongata which usually join into a plexus known as the
hypoglossal nerve.

(2) A variable number of myotomes following the ear
(beginning with somite 4) have disappeared in gnathostomes and
with them have disappeared the somatic motor nerves.

(3) Throughout this region the general cutaneous, splanch-
nic sensory and splanchnic motor components are wholly separ-
ate from the somatic motor component. This is the condition
which persists throughout life in the whole body in Amphioxus.

(4) Usually these three components are united into a com-
plex known as the vagus or vago-accessory nerve, which sup-
plies the skin, mucosa, and visceral (lateral plate) musculature
of the region following somite 4 and the first branchial arch,
including trapezius musculature, stomach, etc.

(5) The relative position of myotomes and gills has been
so much changed by growth and expansion of one part and
shifting of another that it has been difficult or impossible to
trace any fundamental relationship between the myomerism
and branchiomerism.

(6) The above conditions which obtain in embryos are
further complicated in the adults of many vertebrates by the
secondary addition of vertebral elements to the skull.

Before undertaking a general account of this region it will be
an advantage to give a summary of the conditions in Petromyzon,
of which we have a clear and judicial account by KOLTZOFF.

As noticed above, the medial parts of somites 4 and 5 disappear without forming muscle, the lateral parts form muscles on the dorsal side of the head. All following somites persist as myotomes. The somatic motor nerves of somites 4 and 5 are not found. The nerve of somite 6 seems to innervate somites 4 and 5 for a time, then disappears, and somites 4, 5 and 6 are innervated in the adult by the nerve of somite 7. Following this each myotome has its ventral nerve.

Following the ear there is in the embryo one dorsal nerve root or ganglionic anlage between each two somites, corresponding to Nn. IX, X, Sp. 1, 2, etc., and according to HATSCHEK (44) each of these is represented in the adult by a dorsal ramus. Now since the vagus root contains both the sensory and motor visceral components for all the following branchial segments and since the dorsal ramus is typically general cutaneous in vertebrates, it seems clear that there is present in each segment behind the ear in Petromyzon a general cutaneous root, the series continuing without interruption into the trunk.

The glossopharyngeus is independent in Petromyzon and contains (68) general cutaneous, splanchnic sensory and splanchnic motor components which form the typical rami for the segment containing somite 4 and the first branchial arch, ramus dorsalis, r. posttrematicus, r. praetrematicus, and r. pharyngeus. The vagus is treated by KOLTZOFF as constituted of a full branchial nerve similar to N. IX, innervating somite 5 and br. arch 2, and of a ramus branchio-intestinalis. This later consists of a series of ganglia, one over each gill slit, connected by a longitudinal nerve trunk. From each ganglion arise the three rami which innervate a branchial segment in the typical manner. Each ganglion is formed at least in part at the expense of an epibranchial placode. The nerve trunk is continued backward as the ramus intestinalis.

KOLTZOFF concludes from his study of Petromyzon that the vagus nerve with its ramus branchio-intestinalis is not a compound nerve formed by the fusion of two or more segmental branchial nerves, but is a collector which has taken up the ventral rami of several segments. In this he seems to the writer to

be entirely justified by the facts. The above described condi-
tions seem to indicate clearly that the ancestors of Petromyzon
had in the branchial region one complete nerve in each segment
of the same constitution as the present glossopharyngeus. It
appears that the visceral sensory and motor fibers of the caudal
branchial segments, instead of continuing to reach the brain by
way of the dorsal roots proper to their segments, have progress-
ively changed their course so as to run to the brain through the
root of the next more cephalic segment. This process may
have begun as the result of the expansion of the gill sacs and
growth of branchial arch muscles which served to crowd the ven-
tral rami of the nerves at the caudal end of the gill region.
When the shifting had brought the penultimate gill back to the
level of the ultimate nerve root the fibers of the ultimate ventral
rami shifted their course to the root of the penultimate nerve.
The dorsal ramus was unaffected by these conditions and hence
remained independent. As the process went on progressively
the branchial and pharyngeal rami became united by the com-
mon branchio-intestinal trunk which enters the brain by way of
the vagus root. In Bdellostoma (35, 80) it seems that the
process has gone one segment farther and the rami of the whole
branchial region behind the ear have been collected into a single
root which may be supposed to occupy the place of the glosso-
pharyngeus. The writer sees no reason for the supposition
made by KOLTZOFF that Nn. IX and X in Petromyzon may
have arisen by the division of such a root.

It seems to the writer that this interpretation of the vagus
as a collector, which is so obviously applicable to the cyclo-
stomes, offers the most simple and satisfactory solution of the
vexed question of the vagus region in gnathostomes. Without
going into a detailed examination of the literature, it is evident
that facts directly supporting this interpretation are not wanting
in gnathostomes themselves. So-called dorsal hypoglossal roots,
either as ganglionic rudiments or as fully developed roots and
ganglia, have been described by numerous workers (30, 31,
100, 26, 27, 59, 12). Some of these ganglia undoubtedly lie
in segments whose branchial portions are supplied by vagus

rami. This is probably true of the dorsal anlage *u*, *v*, *w*, *x* described by BRAUS in Spinax; of two ganglia in Acanthias des-cribed by HOFFMANN; an of and uncertain number of the anlages said by DOHRN to be present in all his selachian embryos. In the sheep embryo the hypoglossal ganglion lies over the caudal part of the vagus ganglion and its roots enter the oblongata dorsal to and independent from the roots of the vagus. It is evident from our present point of view that these dorsal roots of occipital nerves are composed of general cutaneous elements alone. As in the cyclostomes, the visceral elements have been collected into the vagus. There is therefore no difficulty arising from the presence of dorsal roots in those segments which possess ventral rami from the vagus. In fact, the presence of a dorsal general cutaneous root is to be expected to fill out the complement of functional divisions, and only its absence re-quires a special explanation. Where it is absent, as it com-monly is from a few segments following the vagus root, two ex-planations are possible. One is that the general cutaneous fibers have been collected into the vagus, which I regard as very improbable since there is no cause for it, mechanical or other. The true explanation probably is that as a result of the reduction of myotomes behind the ear and shifting forward of cervical myotomes, the cutaneous area of the original occipital region has been greatly reduced and the general cutaneous nerve roots have aborted in consequence. The general cu-taneous component of the vagus supplies the skin of this region. It may be added here that, as is indicated in Fig. 10, I believe that the shifting of the vagus root described in a previous sec-tion has resulted in gnathostomes in the absorption by the vagus root of the general cutaneous root of the segment next following the proper vagus segment. This is an entirely differ-ent matter from the process of collecting the visceral nerves. It is rendered probable not only by the consideration of em-bryonic conditions but by two other facts: namely, the large area of skin supplied by the dorsal rami of the vagus between the vagus and first spinal nerve; and the existence of two dis-tinct dorsal rami of the vagus (114, 46) with general cutaneous

distribution. The nerve which has been absorbed in gnatho-
stomes is the one in cyclostomes which HATSCHEK calls
"Vagusanhang" and which KOLTZOFF calls the first spinal.

If the vagus nerve really became a collector of the visceral
sensory and motor components in all the following branchial seg-
ments in primitive vertebrates, the condition of these compon-
ents in gnathostomes is clear. The number of gills has been
reduced and the ramus branchio-intestinalis has consequently
lost the corresponding ganglia and rami. It may be suggested
here in view of the evidence that a much larger number of gills
once existed (Sec. 3), that the ramus intestinalis itself would be re-
garded as a trunk which owed its formation in the first instance
to the collecting process above described. In other words the
ramus intestinalis is the collector of all branchial nerves which
may at one time have existed behind the present gill region.
In accordance with this view the oesophagus and stomach, in-
nervated by the r. intestinalis, would be included in the primi-
tive gill region. KINGSLEY's argument (74) that the stomach is
formed by a rapid expansion of a part of the alimentary canal
immediately following the gills is perhaps to be carried one step
further by adding: a region which had earlier been reduced by
the loss of more caudally situated gills. The effect of the pres-
ent suggestion would be to regard the distribution of the ramus
intestinalis as a measure of the primitive gill region.

The formation of the spinal accessory nerve should be ex-
plained in this connection. The visceral motor nuclei are en-
larged in the oblongata and this enlargement continues into the
spinal cord where it gives rise to the roots of the accessory
nerve. This nerve innervates the trapezius musculature which
is formed from the lateral mesoderm, and the nerve is homolo-
gous with the visceral motor components in the vagus. Its
attachment to the vagus is due to processes similar to those
which brought about the union of the branchial nerves with the
vagus. It has been "collected" and probably at a time when
the pectoral arch was a gill arch. The position of the roots
offers no difficulty, since the true vagus roots in some cases have
a similar position ; that is, more or less spread out along the

medulla oblongata and between dorsal general cutaneous roots and ventral somatic motor roots. The accessory illustrates the method by which the collection of motor roots may take place. The shifting of motor roots obviously can not be due *directly* to such peripheral causes as the crowding together of rami which explained the collection of sensory nerves. The motor roots must have been collected under the influence of the sensory components and so indirectly on account of the same causes. As the motor fibers grow out from their nuclei in the brain they must follow some path of low resistance in travelling to their muscles. Since the motor fibers develop late they find such a path already provided in the near-by sensory root. The motor fibers follow this and a mixed trunk is formed. When the sensory fibers of a given root shift their course between the epibranchial ganglia and the brain to the root next cephalad, the motor fibers on issuing from the brain find no path in that segment but must turn forward to the next cephalic sensory root and follow it. As this goes on gradually from segment to segment there are formed a number of roots emerging from the cord or brain caudal to the complex and running along the side of the brain to join it. This is the description of the accessory roots. The more cephalic roots have become more compactly arranged and their fibers run backward within the brain, parallel with the somatic motor fasciculus, to their nuclei of origin. This is the description of the vagus motor roots. Both vagus and accessory motor roots are formed by the same process and constitute a graduated series.

This is a very brief summary of views on a complex region to which hundreds of pages have been devoted by observers in this special field. But even from this it must be evident that the region between the head and trunk is one of transition and the attempt to set a caudal limit to the head which shall be valid for all vertebrates is a fruitless one. Reduction and loss of myotomes with loss of somatic motor nerves, reduction of cutaneous area and nerves, growth and expansion of gills followed by their reduction and loss, shifting and reduction of visceral sensory and motor nerves, shifting of skeletal elements, fusion

of vertebral arches with the skull and secondary separation of the same ; all these and other changes have been seen in this region by various workers and perhaps all have taken place in different degrees in one or another group of vertebrates. The region as represented is almost the most variable in development and structure that can be imagined. No one criterion can be taken by which to determine the posterior end of the head in vertebrates. The caudal end of the skull varies and is of significance only when interpreted in the light of the nerves and other structures. The use of the first nerve which has both dorsal and ventral roots gives widely differing results, and in no case are we sure that the two roots constitute a complete segmental nerve. Myotomes shift, gills are reduced. In truth, the *vertebrate* head has no posterior limit, although such a limit may be more or less arbitrarily agreed upon for any individual vertebrate species.

What is needed now in the study of this intricate region is the analysis of its nerves into their components, the discovery of the source of each component and the tracing of its history, and the determination of the segmental position of each nerve and ganglionic anlage with reference to the series of somites. A great number of data are already available for this but nearly all of them must be interpreted in the light of principles which were not appreciated by the original authors. It would not be profitable at this time to attempt to work over this material because there are too few researches in which the myotomes are certainly identified by reference to a standard series such as v. WIJHE's, and because the nerve roots and anlages are not located with reference to the somites. This material has been treated in a comparative manner by FÜRBRINGER (35) and his vast work might have cleared up this intricate region if he had understood the relations of the components in the sensory nerve roots. As the writer has pointed out elsewhere (70) he failed to appreciate this. There are indications that the relations in this region are not so complicated and the work of unraveling them need not be so arduous as FÜRBRINGER has made it. For FÜRBRINGER the dorsal roots of the cranial and spinal nerves are

homologous; he does not think of the possibility of two separate kinds of dorsal roots being found in the same segment under some conditions. Therefore if nerves of spinal type are found in the vagus region they must have reached their present position by shifting through the long branchial region. As the above discussion has shown, the dorsal and ventral "hypoglossal" roots need not be considered as *spinalartige* nerves. They probably are not equivalent to spinal nerves at all but are only the general cutaneous and somatic motor components of nerves of the vagus region, the visceral sensory and motor components of which have been collected into the single large vagus root. The presence of these nerves in the vagus region, then, does not require the hypothesis that they have shifted forward from the postbranchial region but is directly opposed to such a hypothesis. So far as these nerves are concerned a shifting forward of trunk elements into the head simply has not occured. The nerves are just where we should expect to find them if no shifting or other modification has taken place. This fact is of course not inconsistent with the observed shifting forward of trunk myotomes and the fusion of vertebral elements with the skull. As stated elsewhere, the disappearance of the spino-occipital nerves is due to the reduction of their innervation territory concurrent with the shifting forward of trunk elements. The structure of the nervous system is opposed, however, to the view which supposes that the vertebrate head once (palingenetic) included all the structures innervated by the vagus and the segments in which they were situated, and that all structures now found in the vagus region and not innervated by the vagus have moved forward from the trunk. Owing to the formation of a rigid cranium to protect the brain and sense organs and the secondary extension of this cranium farther caudad by the fusion of more or fewer vertebral elements to the cranium, there has been a reduction of unnecessary myotomes and a shifting forward of trunk myotomes to gain attachment to the cranium. This may be ground for recognizing a coenogenetic cranium; but the cranium is not the head. The shifting of any organ is relative to all the others. The expansion of the branchial ap-

paratus may be expressed as a shifting backward with relation to the vertebrae and muscles, and when the consequent shifting of the heart and blood vessels and other organs (see HOFF-MANN, 60) is taken into account it is an open question whether the shifting backward has not been greater than the shifting forward in the vertebrate body. Shifting should be referred to organs which are known to have some cause for movement with reference to all the others, as the heart is pushed backward by the branchial apparatus, and the trunk myotomes are enabled to push forward by the reduction of those in the head. The analysis of the nervous system and the description of the components present in each of the spino-occipital nerves is the best guide to the explanation of this region. Now that we know the comparative anatomy, much more is to be gained by the study of the actual shifting of organs in the ontogeny than by further speculation.

It is probable that all attempts to divide the vertebrate body transversely into primitive regions will have to be given up. The whole trend of reasoning in the present paper has been against the idea of palingenetic and coenogenetic head regions (GEGENBAUR-FÜRBRINGER). Three main objections to this hypothesis may be stated : (1) in Petromyzon the development of the mesoderm clearly indicates the existence in ancestral vertebrates of a continuous series of similar muscle segments throughout the head and trunk. There is no limit to the palingenetic head to be found in the mesoderm. This seems to be the best key to the interpretation of the conditions in selachians and higher vertebrates as well.

(2) It is by no means certain that the pharynx with its gill slits was confined in primitive vertebrates to the palingenetic head. There are indications that the gills once extended far into the trunk and that the specialization of the branchial nerves had its beginning from that condition.

(3) The interpretation of the nervous system from the functional point of view strongly favors the view that the ancestral vertebrate had a very slightly specialized head region. It is certain that the fundamental divisions of the nervous system

in the trunk region find their exact counterparts in the palingenetic and also in the coenogenetic regions of the head, although with various modifications in different classes of vertebrates. There is good reason for thinking that the special sense organs of the head, their nerves and brain centers, are modifications of one or other of these fundamental functional divisions and not in any sense new structures. The so-called palingenetic head does not have distinct boundaries and is not constituted of distinct and characteristic structures.

Recently FRORIEP (33, 34) has stated his objections to the theory of the palingenetic head, insisting especially that it is false to suppose that there was first developed a primordial head and that this was then modified by various processes of reduction, shifting and dovetailing by which the coenogenetic head was added to the palingenetic. The triple division of the body which he adopts in common with v. WIJHE rests on a scarcely better foundation. The regions are ill-defined and the distinctions between them are traceable to processes which are still indicated in the ontogeny of vertebrates so that the divisions can not be regarded as primitive. The achordate and caducichordate regions are specialized through the reduction of the mesoderm and this is due to the development of the definitive mouth (neostoma) and the reduction of the paleostoma.

13. The morphology of the visual organs.

It is important in approaching the subject of segmentation in the rostral part of the head to have in mind all the structures which have segmental significance. The entoderm and mesoderm of this region have been discussed above. The anterior head cavities of PLATT and a median prolongation of entoderm are the only structures of segmental value afforded by these two germ layers. When we turn to the ectoderm and brain we find in addition to the two so-called nerves of special sense, the optic and olfactory, the nasal epithelium itself and a placode which comes to form the lens, two vestigeal nerves, the N. thalamicus of PLATT and the N. olfactorius accessorius of PINKUS and LOCY, and two epiphysial organs, not to mention several epi-

branchial placodes of doubtful character described by v. KUPFFER. Do all of these organs belong to the one segment represented by the anterior head cavities, or are most of them to be regarded as organs without segmental significance? It seems to the writer that the nervous structures represent more segments than have been preserved in the mesoderm. In other words, there are preserved vestiges of nerve structures belonging to segments whose entodermal and mesodermal organs have disappeared for the most part. The physiological relationships and the structure of these organs should give the clue to their segmental relationships. The division of the brain wall of this region into four neuromeres in embryos of selachians, teleosts and the chick gives a clue to the number of segments.

A full consideration of the visual organs is important for any scheme of segmentation. The paired lateral eyes arise from the lateral surface of the brain tube and remain attached by a hollow stalk to the second neuromere of LOCY—in higher vertebrates the cerebral segment. The stalk becomes replaced by the optic tract whose primary place of ending in the brain is the optic lobes. Comparative studies (37) show that there are two epiphyses in vertebrates, one caudal to the other, both of which possess the structure of visual organs with nerve cells and fibers often present in the adult. These two organs are described as hollow outgrowths of the dorsal wall of the diencephalon. The anterior one in Petromyzon, Acipenser, and reptiles sends nerve fibers into the ganglion habenulae ; the posterior one in Petromyzon, selachians, teleosts, Amia, Anura and reptiles sends its fibers back to the posterior commissure. It is probable that they end in the optic lobes. Such being the general description of the visual organs, have they any relation to other sensory structures and what is their morphological and segmental significance?

The lateral eyes are physiologically related to the skin and the general cutaneous sensory system. Both retina and skin receive stimuli from the external world and both are sensitive to light. It has been shown experimentally by PARKER (102) that the skin of the frog is sensitive to light and that in a degree

sufficient to enable the animal to orient itself with reference to the source of light. The skin of many other animals also has been shown to be sensitive to light. It may be added that the retina is sensitive to pressure, sending an impulse to the brain which is there interpreted as light.

There are certain resemblances between the eyes and the general cutaneous ganglia in the mode of their development. In Petromyzon (76) the eye appears first as a solid outgrowth of the wall of the brain and the cells have the appearance of migrating cells. In this there is a similarity to the mode of formation of the trigeminus ganglion (76, figs. 4 and 7). In selachians, on the other hand, both the optic vesicle and the ganglia of the cranial nerves appear as hollow buds or outpocketings of the brain wall. This has been mentioned by HOFFMANN (59) and a comparison drawn between the eye vesicle and the ganglia in this regard. His figures suggest very strongly that something more than an accidental resemblance obtains. In amphibia (29) the eyes appear first as pigment spots toward the margins of the cephalic plate where a certain rearrangement of cells takes place long before the vesicles begin to bulge out.

From their position in amphibia one would think that the eyes were dorso-lateral structures belonging to the same neuromere as that to which the stalk is attached after the vesicle is formed. This appears more clearly in the selachians figured by LOCY (125). In all vertebrates the vesicle includes a large part of the lateral wall of the fore-brain and owing to the constriction taking place from above downward the stalk comes to have a ventral position. The mode of formation of the optic stalk strongly suggests that the vesicle was not originally a ventral structure, as it is usually regarded, but rather a dorsal one whose attachment to the brain has moved downward or been constricted downward, as happens in the ontogeny. In Lepidosiren (72), indeed, this process is recapitulated in much fuller form than in most vertebrates. The solid optic process appears at first extending laterally from the dorsal wall of the brain. A cavity appears in it and becomes continuous with the cavity of the fore-brain. ''And at the same time, by differential growth, the

attachment of the optic stalk becomes carried downward to the ventral side of the brain." The figures clearly illustrate this as a progression of the optic stalk from the dorsal to the ventral side of the brain. When this is taken together with what is said below about the optic tract I think it will be seen to have considerable significance. At all events the idea that the eye is a dorsal structure involving the dorso-lateral wall of the brain, rather than a ventral one, is of the first importance, if true. I believe that the ontogeny favors this view, although the opposite has been universally held. In correlation with this I wish to point to an important fact in the gross anatomy of the forebrain. In all lower vertebrates there is between the prosencephalon and diencephalon a very slender region made up chiefly of fiber tracts. This slender portion is due to a very deep indentation of the dorsal-lateral wall of the brain above the optic chiasma, and the choroid plexus is widest at this point. This slender region becomes less noticeable in higher vertebrates, where the fore-brain grows larger and more rapidly, but it is clearly seen in embryos and is marked in the adult by the wide choroid plexus. The facts suggest that the nervous material of the dorso lateral wall of the brain tube has been withdrawn in this region and its place is filled merely by a thin membrane. I believe that this is due to the formation of the optic vesicle and that the nerve centers which are recognized as constituting the retina have been derived from the brain at this point, namely in the caudal portion of the fore-brain dorsal to the permanent attachment of the optic stalk.

If we turn to the central relations we shall find a number of very significant facts which explain this relation of the optic vesicle to the brain wall. The optic tracts form a decussation in the ventral wall of the brain which in lower vertebrates is complete and simple. These tracts then enter the optic lobes which were primitively their sole place of ending. These lobes are also the place of ending of the internal arcuate fibers (tractus bulbo-tectalis) from the general and special cutaneous centers in the medulla oblongata. These tracts from the retina and from the cutaneous centers constitute primarily the only afferent

tracts to the optic lobes. The inference is that the optic tracts are to be compared with the internal arcuate fibers. In support of this inference further facts are obtainable in the fish brain. The first is the intimate relation between the two sets of fibers at their place of ending in the optic lobes. The writer has thought that he could distinguish in Acipenser the sets of cells which served as the center for the optic fibers from those which served as the center for internal arcuate fibers. This distinction is at best a difficult one, can not be extended to the whole of the tectum opticum, and is much more doubtful in Petromyzon (68) and selachians (63). It is to be noticed, however, that the structure which corresponds to the colliculus of higher forms is partly differentiated from the tectum opticum in Acipenser and teleosts and is related to the secondary cutaneous fibers only and not to those of the optic tract. From these facts it must be thought that the tectum opticum was in primitive fishes the common center for the optic tract and the secondary cutaneous tracts and that a differentiation into two centers is in progress in the higher fishes.

A second fact is found in the examination of the two chief ventral decussations of the brain, the ansulate commissure and the decussations of which the optic chiasma forms a part. Although both of these (especially the latter) require further investigation, this much may be said: both contain secondary and tertiary somatic sensory tracts destined to the same or similar centers. The most important and primitive tracts in these decussations are:

Chiasma and postoptic decussation.	*Ansulate commissure.*
Secondary: optic tract	Tractus bulbo-tectalis (int. arc.).
Tertiary: tractus tecto-lobaris	Tractus tecto-bulbaris et lobaris
? : tractus lobo-bulbaris	Tractus lobo-bulbaris

The correspondence between the second and third elements suggests that the two decussations belong to one commissural system which has been interrupted by the downgrowth of the inferior lobes. Reasons were given in a previous paper (69) for thinking that the inferior lobes are constituted of cells belonging to the category of commissural and tract cells which are found

in the cord and oblongata.   Whether the homology is correct
or not, it should be noted that the inferior lobes are formed as
an expansion of the mid-ventral part of the brain wall, their
cavity being the greatly expanded ventral furrow of the third
ventricle ventral of the thalamic nucleus of the somatic motor
fasciculus.   Fig. 1 shows this relation.   An expansion ventro-
laterally of this part of the brain wall would very naturally cause a
separation of the ventral commissure belonging here into two
parts, one running in front and the other behind the inferior
lobes.   The homology of the tractus lobo-bulbaris is suggested
in Fig. 7 by the symbols used, but the question of this homo-
logy does not affect the present argument, since the tractus lobo-
bulbaris is present in both decussations.

The presence of centrifugal fibers from the tectum to the
retina should receive explanation in a hypothesis regarding the
origin and morphology of the eye.   From the study of the cu-
taneous centers in lower vertebrates the writer has been led to
suggest (69) that these centers primitively possessed a co-ordin-
ating apparatus consisting of fibers which arose in the dorsal
horn, decussated in the ventral commissure and ended in the
dorsal horn of the opposite side at a higher or lower level.   It
was supposed that these fibers have gradually passed farther
forward until they came to form the tractus spino- et bulbo-
tectalis which ends in the tectum opticum.   The cause of the
shifting forward and concentration of this system of fibers would
be found in the development in the cord of the tract cells which
serve the same function more directly, and in the growth for-
ward of the ascending branch of the cutaneous root fibers in the
dorsal tracts to the medulla oblongata.   Upon this supposition
it will be seen that the centrifugal fibers in the optic nerve would
represent the fibers passing from the cutaneous center of one
side by way of the ventral commissure to the cutaneous center
of the other side in a more cephalic segment ; in this case, from
the tectum by way of the chiasma to the retina of the other side.
The fact that the centripetal fibers of the optic tract pass back-
ward to reach the tectum as a co-ordinating center is explained
simply by the fact that the cutaneous center of the only neuro-

mere rostral to the optic vesicle has never been highly developed and the tectum has early become specialized as a co-ordinating center. Whether this explanation of the centrifugal fibers shall prove to be supported by further investigations of the cutaneous centers, the main fact remains that the tracts which connect the retina with the brain are closely similar to those which connect the cutaneous centers with the tectum, and that the rise of a large general cutaneous nerve (the profundus) in connection with the tectum in the ontogeny indicates that the tectum was originally a primary general cutaneous center.

Following this line of thought it is possible to see in the retina two chief layers which may correspond to the ganglia and central nucleus respectively, and also to draw some comparisons between the cells of the retina and those of the cutaneous sensory centers. The outer nuclear layer with the rods and cones may be thought to represent a general cutaneous ganglion. The outer molecular layer is the place of meeting of the central axones of these ganglionic cells with the dentrites of central cells, and as such suggests comparison with the substantia gelatinosa. The bipolar rod and cone cells of the inner molecular layer correspond to the small cells characteristic of cutaneous centers which in the cerebellum and acusticum of fishes become specialized as granules. The horizontal cells may perhaps be compared with the simple II type cells in the cerebellum and other cutaneous centers. The large cells of the ganglion cell layer correspond to the large cells of cutaneous nuclei which give rise to internal arcuate fibers. The comparison of the afferent and efferent fibers has been made above. It may be said further that there is even a correspondence between the retina and the cutaneous centers in the relative position of the nerve elements. Beginning at the original outer surface of the ectoderm we find in each case the elements in the following order: the primary receptive elements or ganglion cells, the substantia gelatinosa, the small distributing cells of the sensory center, and the large cells whose axones go to other brain centers. These fibers travel at first next to the original inner surface of the ectoderm and as they pass to the opposite side through the ventral com-

missure and longitudinally to enter the tectum they remain "outside" of the central grey, that is near the original inner surface of the ectoderm. When we take into consideration the morphology of the optic stalk and the process of the brain ventricle which it contains, the course of the optic tract fibers from the retina to the brain is comparable in every respect to that of the internal arcuate fibers from the cutaneous centers to the tectum opticum. The migration of the optic stalk from the dorsal to the ventral wall of the brain is now readily understood. The retina must be carried out some distance from the brain wall in order to reach the surface of the head. Since the centers are carried out in the retina the stalk consists only of internal arcuate fibers running through the ventral commissure. These shift to the ventral wall as a matter of economy since in their original position they must follow two sides of a triangle. Furthermore, it will be noticed that if the retina is derived from the dorso-lateral wall of the brain its inner wall which becomes thin is originally continuous with the choroid plexus and the dorsal border of the outer wall of the retina may be regarded as the dorsal border of the brain wall. In this respect the retina is analogous to the acusticum which forms the dorsal part of the wall of the oblongata, and the choroid plexus of the fore-brain is analogous with that of the hind-brain. We could say homologous instead of analogous except for the presence of the equivalent of the peripheral ganglion in the retina.

Finally, reference may be made again to the fact that a frog is able to orient itself with reference to the source of light which falls on the skin alone. It is even shown (102) that the animal orients itself in the same way by means of the skin as by means of the eyes, namely turns its head toward the light and jumps toward it. This shows a close relation between the central paths involved in motor reflexes in response to impulses received from the skin and those received from the eyes. The writer believes that the same paths were originally used for coordinated reflexes by way of the tectum and the fact that these relations are retained in an animal so highly developed as the frog is a strong argument for the fundamental unity of the

visual and cutaneous apparatus in primitive vertebrates. The specialization of the secondary and tertiary centers, visual and cutaneous, we see beginning in the fishes and going on in the higher classes of vertebrates.

We may sum up these several lines of evidence in the following hypothesis. *The retina belongs morphologically as well as physiologically to the cutaneous sensory system. It consists of the general cutaneous ganglion and corresponding centers belonging to neuromere* ii, *which have passed out of the brain wall in order to remain exposed to the light. The optic tract is homologous with the internal arcuate fibers of the cutaneous centers.*

Reference may be made here of a possible comparison of a part of the retina with the acustico-lateral system. It will be seen that in the above there is supposed to be included in the neural tube when it rolls up all that area which at the level of the acustico-lateral anlage is supposed to be left out. The thought quickly presents itself that perhaps the rod and cone cells are homologous with the neuromast cells in the acustico-lateral sense organs, the supposition being that both are derived from cells of the original neural plate which have the power to develop into special sense cells. The presence of sense cells in the saccus vasculosus of lower vertebrates (67, 9, 8) gives color to this supposition although they are situated at the median line instead of the lateral border of the neural plate. The writer sees one morphological objection to this modification of the above hypothesis; namely, that the rod and cone cells are bipolar ganglion cells and not merely sense cells. Another objection is that we have no evidence on the physiological side of close relation between the neuromast cells which are specialized for pressure sense and the rods and cones which are sensitive to light waves. Since we have experimental evidence of a close physiological relation between the general cutaneous ganglion cells and the rods and cones, the writer is inclined to accept the hypothesis in the more simple form stated obove.

The writer has read with great interest BOVERI's effort (10) to connect the eye of vertebrates with the simple invertebrate eye through the pigment spot of Amphioxus. The hypothesis

which he sets forth does not deal with the same field as that which I have dealt. The two hypotheses may prove to be consistent. At one point, however, they are absolutely opposed. BOVERI bases his reasoning on the assumption that the eye, both in Amphioxus and in vertebrates, is a ventral structure. I have supposed, for reasons stated, that the vertebrate eye is a dorsal structure. If the eye of Amphioxus is necessarily to be regarded as a ventral structure, I doubt whether there is any relation between the eye of Amphioxus and that of vertebrates.

Morphology of the lens.

At this time when the lens is being made the subject of experimental investigation it would not be profitable to discuss whether it belongs to the series of epibranchial placodes, or to the dorso-lataral series, or is a structure of an entirely different character. KUPFFER'S hypothesis that it is a modified epibranchial placode fits very well with the absence of the gill slit and the visceral rami to which such a placode would belong. On the other hand, the invagination of the lens suggests relation to the lateral line organs and the auditory vesicle. This is strengthened by the fact noted above that in Gymnophiona the placode of the supraorbital lateral line nerve forms first as a vesicle like the auditory vesicle.

Morphology of the pineal organs.

In spite of the great number of investigations bearing upon these organs they still remain only imperfectly understood, owing probably to their very rudimentary character. In addition to their general structure which fits them to be light percipient organs, two facts point to a relation between these and the lateral eyes. These facts are the presence of rods or cones in Petromyzon (116) and the presence in the lateral walls of the diencephalic and mesencephalic neuromeres of pouches similar to the optic vesicles which may develop into the epiphyses (84, 125). If the epiphyses are formed from lateral pouches of the brain wall, as seems probable, it is not known whether a pair of such pouches fuse to form a median organ, or one of the

pair disappears while the other moves nearer the middle, or whether one or the other process may occur in different forms. More important for the question of segmentation is the fact stated above that one epiphysis is situated behind the other. Since the anterior one has its stalk and center in the diencephalon, it may be assigned without hesitation to the diencephalic (iii neuromere and head segment 3. If the posterior one is one segment farther back it must fall into the anterior of the two mesencephalic neuromeres (iv) and head segment 4. This is consistent with the fact that its fibers pass (apparently) into the optic lobes. It must be noticed, however, that since the stalk of this second epiphysis stands between the superior and posterior commissures its assignment to neuromere iv implies that the anterior limit of the mesencephalon is not the posterior commissure, which has been taken as the most convenient mark. The limit must lie between the two epiphyses, some distance in front of the posterior commissure.

On the supposition that the epiphyses are homologous with the lateral eyes, and the evidence is all in favor of this, the writer would consider them to be metamorphosed cutaneous ganglia belonging to the third and fourth neuromeres and head segments. In the case of the epiphyses, their wholly dorsal position, the direct entrance of the fibers into dorsal centers without a chiasma, and the presence of the cutaneous center (tectum) in the segment of the second epiphysis all indicate that the cutaneous centers have remained in the brain. It seems probable that the centers for the first epiphysis have degenerated with the reduction of the organ. This view is suggested by the fact that in Petromyzon, where the organ is functional, the left ganglion habenulae divides into an anterior part which comes into connection with the epiphysial vesicle, and a posterior part which receives the tractus olfacto-habenularis through the superior commissure. The finding of these facts in Petromyzon changed the view which I had formed from the study of Acipenser, namely that the ganglion habenulae had changed its function after the reduction of the epiphysis. The structure and relations of the ganglia habenulae can be better

explained on the assumption that they belong to the central grey.

14. The nerves of Platt, Locy and Pinkus.

Miss PLATT found in Acanthias (106, 107) a process from the neural crest at the groove between the mesencephalon and diencephalon which later disappeared. She believed this to be the vestige of a nerve which was formerly developed, and gave it the name N. thalamicus. Its history has been followed more completely by HOFFMANN (58, 59). The strand of neural crest cells descends over the optic stalk and meets the profundus strand at a point where later the ciliary ganglion is formed, and then loses its connection with the brain. Since the profundus ganglion is distinct from the ciliary and is formed from a different part of the neural crest, it seems altogether probable that the ciliary ganglion permanently represents the N. thalamicus. KUPFFER (79) finds the same structure forming the ciliary nerve in Ammocoetes. HOFFMANN describes a small cutaneous branch from this ganglion but it is not clear that it is not composed of profundus fibers. In the case of the ganglion ciliare we seem to have the formation of a sympathetic ganglion from the ganglion of a nerve which has otherwise aborted. Since the sympathetic is derived from the visceral sensory and motor systems, we may consider the N. thalamicus as the vestige of a splanchnic sensory nerve root. In position it corresponds to the second epiphysis and lies one segment in front of the profundus. It would therefore belong to the first mesencephalic neuromere. The N. thalamicus may be considered as the splanchnic sensory nerve of neuromere iv and head segment 4.

PINKUS (104) described a nerve in Protopterus which arose from the brain in the vicinity of the praeoptic recess and, running forward, was distributed to a part of the olfactory epithelium, mingling with the olfactory nerve fibers. LOCY (85, 86) has described the development and anatomical relations of a nerve which he has found in 19 genera of selachians. In most of the genera described the nerve enters the ventral surface of the fore-brain, in several it enters the dorsal surface near the anterior

end. The nerve has the same distribution as the nerve of PINKUS and is considered by LOCY to be homologous with it. LOCY's nerve possesses a distinct ganglion and ends centrally in a mesial eminence of the infolded pallium (126).

Until this nerve is better understood it is not worth while to attempt to explain the difference in its point of attachment to the brain in different species. It is important to notice, however, that its adult position indicates that it arises either lateral or dorsal to the neuropore in selachians. Its position is therefore morphologically dorsal and both the position of its root and its distribution to the extreme anterior end of the head indicate that it belongs to the first segment. Since it is distributed to the skin it may be supposed to be general cutaneous in character. Until further investigation, then, the hypothesis is suggested that the nerve described by PINKUS and LOCY represents the primitive general cutaneous nerve of the first segment.

If it is true that this nerve ends in the pallium in selachians, the fact suggests the very interesting possibility that before the olfactory cortex was developed a general cutaneous center was located in its place. More than this can not be said until the central relations of the nerve are more fully studied.

15. Morphology of the olfactory organ. Functional and morphological relations to the gustatory system.

The resemblance of the olfactory sense cells to the typical sense cells of segmented worms may be taken as a starting point. Since the ectoderm of these worms is provided with free nerve endings (113, 110, 82) comparable to the general cutaneous endings in vertebrates, the sense cells probably do not have a tactile function. It is more probable that they serve the function of taste or smell. Or perhaps it would be better to say that they have an indifferent chemical sense. These cells are especially numerous in the prostomium and roof of the mouth in the earth-worm. In Amphioxus (24) such cells are present as scattered cells in the lining of the buccal cavity, the velum and tentacles, the oral cirri, and the skin of a large part of the body; and in the form of cell groups or organs they are found in the

cirri and velar tentacles. The region in which the olfactory epithelium is formed in vertebrates corresponds closely in position to HATSCHEK's pit in Amphioxus. This is based upon the description of v. WIJHE (120) and LEGROS (83). This pit lies in the roof of the invagination which corresponds to the hypophysis of vertebrates. It follows that HATSCHEK's pit of Amphioxus and the olfactory organ of vertebrates lie in the roof of the ancestral mouth and in this position correspond to the prostomial area of invertebrates in which sense organs are especially numerous. The hypothesis is suggested, therefore, that the olfactory organ represents a collection of sense organs of the type found in segmented worms which at first was related to the vertebrate paleostoma as the special collection of sense organs is related to the annelid mouth. These organs probably had an undifferentiate chemical sensibility and served the worm and the primitive vertebrate in seeking food. It is not necessary to this hypothesis that HATSCHEK's pit should prove to be a sense organ in Amphioxus. The reference to it is made only for the sake of indicating as clearly as possible the point at which the sense cells are supposed to have collected.

The question of the segmental value of the olfactory nerve was discussed in a previous paper with the result of denying it primary segmental value. This was based on the description of its nerve centers and the specific conclusion reached was that the olfactory nerve and its centers cannot serve to define the segments in which they lie because they have no resemblance to the typical nerves. I see no way to minimize that argument but it may be said nevertheless that we have in the first segment of the head in addition to a general cutaneous nerve a nerve whose functions are visceral sensory. And now I may go further and suggest how the very differences between the olfactory apparatus and the other cranial nerves may be taken to indicate the morphological status of the region of the head in which it is. If the comparison of the olfactory epithelium with the special collection of sense cells in the prostomium of annelids is accepted, it implies that the olfactory segment is equivalent to the invertebrate prostomium. So far, then, the writer is in-

clined to think that the olfactory organ and nerve are peculiar in the vertebrate organization. In the figures, however, these structures have been indicated by the same symbols as the visceral sensory system, on the basis of the visceral function of the olfactory apparatus.

On the basis of their function the writer has for several years felt impelled to seek some morphological connection or relation between the olfactory apparatus and the visceral sensory, especially the gustatory. After what has just been said this search would seem contradictory, if not fruitless. However, we have not yet sufficient knowledge of these systems to warrant our jumping to any final conclusion. Even if the first segment of the vertebrate body is a prostomium, its general cutaneous innervation is homologous with that of the rest of the body. May not its visceral sense be related to that of the typical segments also? The writer has in his notes detailed statements of several hypothesis, but it will be more profitable in the present state of our knowledge to indicate briefly one or two lines along which facts may be sought, than to spend time in speculations.

(1). When the gustatory paths and centers within the brain are known at least as well as we know the olfactory we may find some indications of their relationship.

(2). If we were to apply to the epibranchial placodes the theory of KUPFFER which the writer has declined to accept for the dorso-lateral placodes, some such line of reasoning as this might be developed. The cells of the chemical sense which are scattered over the body in annelids may have collected over the gill slits in primitive vertebrates. These collections would form the primary sense organs of KUPFFER. These sense cells sink below the surface as ganglion cells. Secondary sense organs develop in the placodes and these become the taste buds. If we suppose that the primary sense cells sent their fibers to the brain along with the general visceral rami which pass adjacent to the gill slits, we have a close relation shown between the gustatory and olfactory systems. It should be noticed, however, that in this statement as it stands no homology is shown be-

tween the centers of the two systems, since it is by accident that the taste fibers enters the visceral centers.

(3). If the dorso-lateral placodes represent a part of the neural plate area of ancestral vertebrates, may not the epibranchial placodes be an offshoot from that also? This suggestion would have a point if it were shown that the end buds had their origin from the epibranchial placodes as the neuromasts have their origin from the dorso-lateral placodes. It would be necessary to explain further the wide separation between the epibranchial placodes and the neural plate, and the permanent relation of the nerves of these placodes, not to the margin of the neural plate but to the column which lies mesial (ventral) to the cutaneous area of the plate.

(4). The following suggestion seems to the writer most in accord with such facts as we have at present. The end buds are recent organs, formed comparatively late in the phylogeny. They appeared first in the vicinity of the mouth and gill slits where they would detect indications of food in the respiratory water current. In this position relative to the vertebrate neostoma they would supplement the impressions received from the olfactory organ. The animals in which end buds first appeared may be thought of as relatively inactive, so that the respiratory current formed their chief source of information as to the presence of food. They were distinguished from such animals as Amphioxus which feed by means of cilia by the fact that they captured larger kinds of food by muscular movements. This would be accomplished at first by means of the visceral muscles of the jaws and branchial skeleton alone, the food perhaps being sucked in by a sudden increase of the respiratory current. The innervation of the end buds was determined by their function. It is evident that they could not be innervated by the general cutaneous component. For, if cutaneous fibers could receive and transmit impulses due to chemical stimuli those impulses would be interpreted in the brain as tactile impulses; that is, they would give rise to reflex movements which characteristically follow upon tactile impulses. In the present case this would be useless or harmful to the animal. On the

other hand impulses transmitted by the general visceral sensory fibers would be followed by reflex movements of the visceral musculature. Since the visceral fibers passed close to the supposed site of the first end buds, their innervation by these fibers is easy to understand. As the end buds became more numerous and important they spread into the mouth and over the head and body and the visceral nerves followed them. While it is not possible to explain in detail the arrangement of these nerves, the disposition of such nerves as the ramus recurrens facialis in teleosts is in support of this view. If any relation is to be found between the gustatory and olfactory systems it must rest upon the central relations of the two systems. If the gustatory centers and fiber tracts are so related to the olfactory as to show that the primary olfactory centers belong to the same longitudinal zone of the brain as the visceral centers, the close physiological relations between the olfactory and gustatory organs have their explanation in their morphological relations. The writer expects that this will prove to be the case and in another section offers some slight suggestions looking in this direction.

16. The first four head segments.

These may be passed over briefly since all of the structures concerned have been treated in the above general discussion.

a. Segment 4.

Neuromere **iv,** anterior head cavity, palatine arch (?), epiphysis 2, N. thalamicus (ciliary ganglion and nerve), lens placode (?).

The structures peculiar to this segment are all rudimentary. Only the brain is well developed and that chiefly because of its relation to the cutaneous and optic tracts. The dorsal mesoderm is represented by the anterior head cavity in selachians, the lateral mesoderm only by the palatine arches of KUPFFER in Petromyzon, if they actually exist. The splanchnic sensory nerve is represented by the rudimentary N. thalamicus from which the ciliary ganglion and nerve are derived; the somatic sensory nerve by the second epiphysis. If the lens is developed from an epibranchial placode it should be placed here in con-

nection with the ciliary nerve (79) as the epibranchial placode of the fourth segment.

b. Segment 3.

Neuromere **iii**, most anterior portion of the median entoderm (?), epiphysis **1**.

Neuromere **iii** represents the thalamus but according to HILL's results (52) does not include the hypothalamus which is developed in teleosts as a ventro-caudal expansion of the lower wall of neuromere **ii**. No mesoderm and no motor nerves are present but within the brain is the thalamic nucleus of origin of the somatic motor fasciculus. Its location here possibly indicates the former presence of a motor nerve in this segment; no other explanation occurs to the writer. The representative of the general cutaneous nerve is found in the anterior epiphysis. The innervation of the skin is taken over by the profundus. As suggested above, the central nuclei belonging to the cutaneous division have probably become reduced to an insignificant remnant on account of the degeneration of the epiphysis. The ganglia habenulae in their structure resemble the central grey and they may be regarded as one of the earliest special centers to be differentiated from it. The suggestion has been made earlier (69) that the central grey belongs to the category of the commissural and tract neurones which are found in the oblongata and cord. The reason for the large development of these central elements in the diencephalon is to be found in the reduction of the somatic and visceral sensory and visceral motor centers. The posterior commissure, whose nucleus of origin lies in this neuromere, is spoken of below (Sec. 17).

c. Segment 2.

Neuromere **ii**, lateral eyes, hypophysis.

The interpretation of the eyes as the representative of the cutaneous division has been given above. In the central nervous system important centers are developed. Neuromere **ii** includes the striatum area and also that of the pallium. The writer has previously referred to the striatum as probably representing the tract cells of the cord and oblongata. The nature

of the specialized nucleus known as the epistriatum is a difficult question. It serves in fishes as the end nucleus of two very different classes of fibers. The one comes from the inferior lobes and corpora mammillaria by way of the anterior commissure; the other comes from the cells of the olfactory bulb through a somewhat isolated portion of the anterior commissure. It is probable that this is the more primitive tract and that it is gradually supplanted by tracts from the hypothalamus and perhaps other regions. In any case the epistriatum seems to belong chiefly to the visceral sensory apparatus.

The origin and relationships of the cerebral pallium have been discussed by the writer elsewhere (70). The massive pallium which is related to the olfactory apparatus is regarded as a neomorph in gnathostomes and as such it is not of especial importance for our present subject. It has been suggested above, however, that this olfactory pallium may have been preceded by a structure which was the general cutaneous nucleus of the first segment. The pallium, then, is to be regarded as a new structure developed in the space from which the lateral eyes were derived.

If HILL's interpretation of the neuromeric relations is correct, we are brought to the interesting result that the diencephalon is formed from two neuromeres, the hypothalamus belonging to the same neuromere with the striatum and pallium and lying morphologically ventral to them. The writer has shown that in fishes (Acipenser, 67) throughout the whole length of the ventral wall of this second neuromere the structures adjacent to the middle line (nucleus thaeniae, inferior lobes in part, and corpus mammillare) are histologically identical. In Petromyzon (68) the inferior lobes and corpus mammillare are fundamentally alike, there being but slight differentation. It seems, then, that a single nucleus has been interrupted by the optic chiasma and accompanying decussations. The posterior portion of this nucleus was associated with the saccus vasculosus and also came to receive tertiary tracts from both the olfactory and the somatic sensory centers. It has consequently developed into a large coordinating center. The anterior portion of the nucleus (nuc.

thaeniae) received secondary olfactory tracts and remained at a lower stage of development.

The absence of epibranchial placodes in segments 2 and 3 is noteworthy. If the hypophysis is in segment 2 no placode is to be expected. The absence of one in segment 3 may argue against the supposition that a gill was ever present in that segment. The lense placode and the N. thalamicus would then appear to be the vestiges of the nervous structures connected with the most anterior ancestral gill slit.

Whether the hypophysis is to be assigned to this segment or to segment 1 involves the question whether we are to recognize a prostomium in vertebrates. The hypophysis invaginates about opposite the groove between neuromeres i and ii and extends back beneath neuromere ii. This canal is perhaps equivalent to the buccal cavity of invertebrates. The treatment of the olfactory organ in this paper and the interpretation of the hypophysis as the invertebrate mouth are both consistent with the recognition of the first segmeut as a prostomium.

d. Segment 1.   Prostomium.

Neuromere i, nerve of Locy, olfactory epithelum and nerve.

The writer is unable to accept KUPFFER's idea of a median olfactory organ. It does not appear from his descriptions that the median thickening between the olfactory placodes is ever sensory. Its connection with the brain for some time is to be explained as a mere persistence of the continuity of the neural tube with the ectoderm at the lower edge of the neuropore. The olfactory sense cells exist from the first in bilateral groups and are innervated by paired nerves. As may be inferred from references to Amphioxus made above, the writer thinks that the interpretation of the olfactory pit as a true olfactory organ requires further evidence.

The olfactory bulbs are formed by great growth of the lateral walls of the first neuromere. In lower fishes (67, 1 6) and cyclostomes (68) these bulbs still show a structure comparable to that of the primitive brain wall. The highly speciali zed mitral cells are not primitive features of the olfactory apparatus,

but are neomorphs in craniates which are just beginning their specialization in cyclostomes.

The general cutaneous nerve of LOCY and the olfactory nerve are to be taken together as roughly the equivalent of the nerve of the prostomium in segmented worms.

17. The dorsal commissures of the brain.

In Figs. 1–7 are shown the longitudinal zones of the brain belonging to the four functional divisions of the nervous system. A further review of these zones does not fall within the scope of the present paper. Some remarks upon the dorsal commissures and their relations to the zones, however, will perhaps be of value. It should be said at the outset that the fiber crossings in the brain of lower vertebrates, both dorsal and ventral, are in the greatest part if not wholly mere decussations. True commissures are almost unknown. When the word ''commissure'' is used in the following paragraphs it is used because it has come to be part of the accepted name of a given fiber-crossing.

The dorsal decussation of the spinal cord in higher vertebrates contain splanchnic sensory (sympathetic) fibers, collaterals from cutaneous fibers, and perhaps secondary elements. At the junction of the spinal cord and brain in all vertebrates this decussation is greatly enlarged just behind the choroid plexus of the IV ventricle. This enlarged portion, known as the commissura infima HALLERI, is composed chiefly of splanchnic sensory fibers from the roots of the VII, IX and X nerves. These fibers for the most part end in the median nucleus of the commissure of CAJAL (46, 67, 68). A part of them without crossing (and a part of the crossed fibers also?) pass on back into the spinal cord (68). Other fibers in the commissura infima come from the cells of the nucleus funiculi (90, 46). From these facts it is evident that both splanchnic sensory and somatic sensory elements cross in the dorsal decussation of the cord. The somatic sensory elements are chiefly or wholly secondary fibers, or only collaterals.

These two components must be rigidly distinguished if we are to understand the dorsal decussations of the brain. The

dorsal decussation of the medulla oblongata is not obliterated on account of the non-nervous roof, but its elements are crowded forward or backward. Behind the choroid plexus the commissura infima contains the splanchnic sensory elements proper to the segments of the VII, IX and X nerves. It is probable that the course of the root fibers of these nerves within the brain has been influenced by the crowding backward of their decussation and median nucleus by the choroid plexus. It is further probable that those fibers which take this caudal course are the more primitive components of these nerves, namely the general visceral fibers as distinguished from end bud fibers. It is known that the end bud fibers in teleosts (48) end chiefly in the lobus facialis. The point of especial interest in the present connection is that the concentration of the visceral decussation for the VII, IX and X nerves behind the choroid plexus precludes the expectation that the visceral elements of the first order will be found in the dorsal decussations farther forward. There are no visceral nerves anterior to N. VII.

The somatic sensory elements have behaved differently with reference to the IV ventricle. Instead of concentrating behind it they have concentrated in front of it. In those vertebrates in which the cerebellum is most primitive (Petromyzon, Protopterus, Urodeles) a commissure constitutes a prominent part of it. This decussation consists of axones of granule cells situated in the cerebellum destined to the somatic sensory nuclei of the medulla oblongata. This is therefore to be considered as the homologue of the somatic sensory portion of the dorsal decussation of the spinal cord. It is an important decussation in all lower vertebrates.

A second prominent cerebellar decussation is found in fishes (67). This is situated farther ventrally and cephalad and instead of connecting the dorsal portions or lateral lobes of the cerebellum, connects two nuclei which in fishes lie in the lateral walls distinctly ventral to the somatic sensory centers, the secondary vagus nuclei. The fibers of the secondary vagus tract coming from the vagus lobe end in part in the secondary vagus nucleus of the same side and in part cross

to the opposite side. The remainder of the decussation is formed by axones of cells of these nuclei. The destination of these axones is unknown, so that we are uncertain whether true commissural elements are present. It is evident, however, that the decussation belongs to the splanchnic sensory division of the nervous system.

In mammals the tract which corresponds to the secondary vagus tract is the direct cerebellar tract arising from the cells of CLARKE's column in the cord. This tract ends in a nucleus which lies in the roof of the IV ventricle in the vermis. It is, however, probably homologous with the secondary vagus nucleus of lower vertebrates.

The dorsal decussation of the optic lobes requires but brief mention. In accordance with the interpretation of the lobes given in this and previous papers it must be regarded as a somatic sensory decussation comparable with the somatic portion of the decussation in the spinal cord.

The posterior commissure is a decussation of fibers arising from a nucleus in the dorsal part of the diencephalon and mesencephalon (75, 68). After crossing the fibers run toward the base of the medulla oblongata. The destination of the fibers is unknown, and nothing is known of the fiber tracts which may come to end in the nucleus of origin. The fact that the decussation is somewhat intermingled with the dorsal decussation of the optic lobes suggests that the two may be related. Some of the cells of origin of the posterior commissure in Petromyzon are so situated as to be indistinguishable by their position from those of the optic lobes. Without knowing the connections and functions of the posterior commissure, nothing further can be said.

In the roof of the diencephalon two decussations are present, the well known superior or habenular commissure and a decussation closely related to the base of the epiphysis known only in a few forms (67, 62). The superior commissure contains decussating fibers from the olfactory nuclei of the fore-brain (tractus olfacto-habenularis) and also, according to CATOIS (16) and CAMERON (15) true commissural fibers. A certain similarity

is to be noticed between this and the decussation between the secondary vagus nuclei in the cerebellum. Decussating fibers of the second and third order are present in each case. A further point of comparison is found in the fact that the ganglia habenulae appear to be a part of the central grey some distance removed from the dorsal wall of the brain, which here is a choroid plexus. If we accept the supposition that the somatic sensory nucleus of the diencephalon has degenerated, the morphological position of the ganglia habenulae corresponds rather closely to that of the secondary vagus nucleus beneath the somatic sensory centers of the cerebellum. The choroid plexus of the diencephalon is regarded as morphologically equivalent to the optic lobes or dorsal part of the cerebellum and the ganglia habenulae are morphologically lateral. These hypotheses have a significance in connection with the question of the relation of the olfactory and gustatory organs and centers discussed above.

Not enough is known about the epiphysial decussation to admit of any discussion.

The anterior commissure consists of two distinct parts: a smaller, anterior portion, sometimes isolated, composed of fibers from cells of the olfactory bulb destined to the epistriatum; and a larger portion composed of fibers from the inferior lobes also destined to the epistriatum. A third element, consisting of fibers from the lateral cortex to the opposite epistriatum, need not be considered since it is not primitive in vertebrates. The tract from the inferior lobes is a tertiary tract which may be either olfactory or somatic sensory in character. We have seen reasons for thinking that the hypothalamus has been modified by the entrance into it of the somatic sensory tracts. We must therefore regard the secondary (and tertiary?) olfactory tracts as constituting the primitive portion of the anterior commissure. The writer is unable to see any resemblance between this and the somatic sensory decussation, while there is a certain similarity between the anterior commissure and the splanchnic sensory decussations of the ganglia habenulae and the secondary vagus nuclei. If the anterior commissure is to be compared

with the other brain commissures it is doubtless to be considered as a part of the dorsal splanchnic decussations.

We may summarize the dorsal commissures by saying that the dorsal decussation of the cord has been differentiated in the brain into separate somatic and splanchnic sensory decussations. The commissura infima HALLERI, the decussation between the secondary vagus nuclei, the superior commissure, and the anterior commissure represent the splanchnic portion. The dorsal commissure of the cerebellum, the dorsal decussation and posterior commissure of the mesencephalon constitute the somatic portion. Whether the pallial commissure will be brought into the latter category on account of the relations of LOCY'S nerve remains to be seen.

Some reference was made to the ventral commissures in discussing the morphology of the eye. The writer has nothing further to add.

18. The sympathetic system.

The relation of the sympathetic to the four functional divisions of the nervous system is important in connection with the subjects dealt with in the present paper. Although the sympathetic in lower vertebrates, where we must look for its genetic relations, is very imperfectly understood, yet sufficient is known to indicate that the sympathetic is morphologically related to the visceral divisions. This is what the function of the sympathetic and the central relations of its fibers in higher forms has led us to expect. In the trunk regions in selachians (60) the sympathetic ganglia are budded off from the distal portion of the spinal ganglia after the union of the ventral with the dorsal root. It does not appear that anything is contributed to the sympathetic by the ventral root in fishes. In the adult (64, 98) sensory fibers coming from the viscera pass through the sympathetic and spinal ganglia to end in the region of CLARKE'S column in the cord, and motor fibers arising in the lateral motor nucleus enter the sympathetic by way of the dorsal root (and in higher forms by way of the ventral root also). If we interpret

the formation of the sympathetic ganglia in the light of the adult structure, we must suppose that the spinal ganglion cells which migrate to the sympathetic ganglia are those of the general visceral component.

It is a striking fact which has not passed unnoticed that the composition of the sympathetic closely resembles that of a branchial nerve minus the cutaneous components of the latter. In cyclostomes and selachians no sympathetic ganglia have been found in the head, except the ganglion ciliare. If this be the true condition then in these forms the cranial ganglia must be considered to contain the equivalent of the sympathetic. That they can not as a whole be considered homologous with the sympathetic ganglia of the trunk is obvious from the presence of taste fibers and general cutaneous fibers. In teleosts (46) sympathetic ganglia are present in connection with the typical ganglia of the profundus, V, VII, IX and X nerves, in addition to the ciliary ganglion which is the sympathetic ganglion of the segment anterior to the profundus. The ganglia are connected by a longitudinal fiber strand as in the trunk. The high development of the sympathetic in the head of teleosts suggests that it may yet be found in selachians.

19. Relation of dorsal and ventral nerve roots to the myotomes.

In Amphioxus the ventral root emerges from the spinal cord opposite a myotome and enters the muscle directly. The dorsal root emerges from the cord between two myotomes, passes along the myoseptum to the surface and is distributed to the ectoderm overlying the myotome next anterior to its root. I can add from my own observation that although the ventral ramus (the visceral fibers of which do not concern us here) usually passes vertically ventrad and so crosses the surface of three myotomes, it not infrequently happens, especially in the caudal half of the body, that the ventral ramus runs caudoventrally at the same angle as the myotomes and a single nerve is confined to the area overlying a single myotome.

In Ammocoetes by putting together the work of HATSCHEK (44) and KOLTZOFF we can account for every one of the dorsal

and ventral roots of the cranial and first spinal nerves and can state their origin, relation to the myotomes and distribution. Reference to Fig. 10, with which HATSCHEK's Fig. 11 and KOLTZOFF's diagrams may be compared, will make the relations clear. The profundus passes over the caudal and ectal surface of somite 1, which is innervated by N. III, and is distributed to the ectoderm outside and in front of that somite. The trigeminus passes over the caudal and ectal surface of somite 2, innervated by N. IV, and is distributed to the ectoderm overlying that somite and its mandibular arch. N. VII passes caudal to somite 3, innervated by N. VI, and supplies the hyoid arch. It has no cutaneous component. N. IX lies between somites 4 and 5 and has a dorsal ramus passing out along this septum (HATSCHEK's *Occ. 1*). The vagus ganglion appears between somites 5 and 6 and its dorsal ramus passes out along this septum. There is no ventral root to either somite 4 or 5 on account of the early reduction of the mesial part of each of these somites. Behind somite 6 (KOLTZOFF) both dorsal and ventral roots are present. The ventral root of somite 6 probably innervates myotomes 4, 5 and 6 in the larva. The dorsal root sends a ramus to the skin of the occipital region (*Occ. 3*, HATSCHEK). We should expect the dorsal rami of N. IX, X and Sp. 1 to be distributed to the ectoderm overlying somites 4, 5 and 6 respectively. It is probable that this is their actual position in the embryo but owing to the migration forward of myotomes 4, 5, 6 and 7 during development myotome 5 is brought beneath the ectoderm belonging to somite 4, myotome 6 beneath the ectoderm of somite 5, etc. This accounts for the apparent distribution of HATSCHEK's *Occ. 1*, *2* and *3* to the area over myotomes 5, 6 and 7. These dorsal nerves all persist in the adult but the ventral nerve of somite 6 disappears and myotomes 4, 5, 6 and 7 are all innervated by the ventral nerve of myotome 7. From the work of these two authors, then, it would appear that the relations in cyclostomes are the same as in Amphioxus, the dorsal nerves innervating the ectoderm overlying the myotomes next anterior to the dorsal roots. Two further remarks are to be made. NEAL's suggestion that

N. VI includes the ventral nerve of somite 4 (and that of somite 5 ?) does not affect the the present question. It is an important question, however, whether HATSCHEK's *Occ. 1, 2* and *3* are all general cutaneous nerves. If they are lateral line nerves without general cutaneous fibers they are worthless for the present purpose. The writer has described a branch from the N. lateralis to this part of the skin. The cranial nerves of Petromyzon require to be reinvestigated, but so far as our present knowledge goes the above account of the relation of the dorsal roots to the myotomes appears to the writer to be perfectly sound.

The same relation of the nerves to the somites is found in Spinax (12) where N. IX lies behind somite 4, N. X behind somite 5, and a rudimentary ganglion is formed behind each of the following somites. Six of these rudimentary dorsal nerves eventually disappear owing to the reduction and shifting of myotomes and consequent reduction of cutaneous area.

HATSCHEK in 1892 came to the same conclusion as I have stated with regard to the relation of dorsal roots to myotomes in Amphioxus and cyclostomes. In 1893 he published a brief correction (45) in which he said that in all higher vertebrates the dorsal root unites with the next following ventral root. This can be made out most readily, he says, in amphibian larvae. I have examined such sections of amphibian embryos as I have by me and although I have none old enough to show the distribution of the nerve rami, I find two facts opposed to HATSCHEK's statement. The dorsal roots are always a short distance caudal to the ventral roots, and the ventral roots run across the cephalic face of the ganglia. I do not see how this could result if each dorsal root joined the next following ventral root. I hope soon to investigate the matter farther in Amblystoma.

The second statement of HATSCHEK seems to have been generally accepted by later workers. I am inclined to think that his first statement was correct for the fishes at least.

20. *Comparison of head and trunk.*

Aside from the development of special organs in the head, the chief differences between the head and trunk lie in the skele-

ton and somatic muscles and in the relation of the dorsal and ventral nerve roots to one another and to the myotomes. The formation of a rigid cranium has had very important consequnces in the disappearance of postauditory myotomes and the development of complicated conditions in the occipital region. To this also is due the fact that certain myotomes have been released from their attachment to a segmented skeleton and have come to move the eyeball. It may be said that the same cause has indirectly determined the relation of the nerve roots to the myotomes. In cyclostomes, where the buccal apparatus has demanded the preservation of the dorso-lateral portion of the postauditory myotomes, the nerve roots are covered by these very much as in the trunk. In gnathostomes, however, when postauditory myotomes completely disappear the nerves are given free access to the ectoderm. When trunk myotomes shift forward it is their ventro-mesial portions which become attached to the cranium and so the nerves retain their superficial position. The union of the dorsal and ventral roots in the trunk is a late development and the head has retained the more primitive condition. In the constitution of the dorsal and ventral roots also the head has retained the primitive condition, while the trunk nerves have been somewhat modified at least in higher vertebrates. The dorsal roots originally contained the somatic sensory, splanchnic sensory and splanchnic motor components, as in Amphioxus. In the trunk a part of the splanchnic motor component has come to run in the ventral root and perhaps other modifications have taken place.

SUMMARY OF THE CHIEF CONTENTS.

1. The primitive vertebrate was a segmented animal with probably very slight cephalization.

2. Each segment consisted of derivatives of the ectoderm, dorsal mesoderm, lateral mesoderm and entoderm, and of somatic sensory, somatic motor, splanchnic motor, and splanchnic sensory divisions of the nervous system primarily related to the skin, the myotomes, the visceral muscles, and the visceral surfaces respectively. The definite relations existing between the

functional divisions of the nervous system and the organs severally innervated by them make the nervous system the best guide to the segmentation of the head.

3. The anterior end of the head is indicated in existing vertebrates by the point at which the neural plate meets the general ectoderm and the entoderm, in those forms in which the rostral entoderm is most completely preserved. Lateral to this the olfactory epithelium is formed. Ventral to it the hypophysis represents the vertebrate paleostoma or invertebrate mouth. That part of the head and brain which extends over the hypophysial opening may be compared to the invertebrate prostomium and as such contains only cutaneous and olfactory nerves.

4. It is probable that one or two pairs of gills formerly existed between the paleostoma and the present mouth. This is indicated by the presence of epibranchial placodes and palatine and trabecular arches in Petromyzon, by the mode of formation of the ciliary ganglion, and by the labial cartilages of selachians. Similarly one or two formerly functional myotomes have been lost from the anterior end of the head. The anterior head cavity of selachians is the rudiment of one of these. Another more anterior, is possibly indicated by the somatic motor nucleus far forward in the thalamus. The loss of these several organs has been followed by the loss of the typical nerves or their modification into special sense organs. The nerve of Locy and the ciliary ganglion are the only nerves in the first four segments which retain their primitive relations.

5. Following this region of greatest modification, it is believed that the segments can be reduced to common terms and the segmental position of all the organs determined. See Table B and Figure 10.

a. The gill slits were originally intersegmental.

b. Each typical dorsal root contained a general cutaneous component distributed to the skin; a communis component distributed by way of the posttrematic, pretrematic, and pharyngeal rami to the mucosa; and a visceral motor component to the visceral musculature by way of the posttrematic ramus. The

TABLE B.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
HEAD SEGMENTS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
NEUROMERES	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	xiii	xiv	xv	xvi	xvii
SOMITES			----	a. h. c.	1	2	3	4	5	6	7	8	9	10	11	12	13
BRANCHIOMERES				----	--	mandib. arch	hyoid arch	br. 1	br. 2	br. 3	br. 4	br. 5	br. 6	a larger number of branchial arches in lower cyclostomes and primitive vertebrates.			
SOMATIC SENS. DIVISION *general cutaneous* peripheral central	N. of Locy pallium				N. ophth. prof.	comp't in N. V. shifts to vii	---- [joins N. V?]	comp't in N. IX shifts to ix	comp't in N. X. shifts to x in Gnath.	1 sp. Pet. joins N. X, Gnath.	2 sp. Pet. rudiment in Gnath.	3 sp. Pet. rudiment in Gnath.	4 sp. Pet. rudiment in Gnath.	5 sp. Pet. rudiment in Gnath.; permanent root in Acanthias?	6 sp. Pet. permanent root in Acanthias	7 sp. Pet. permanent root in Gnath.	S sp. Pet. 2 sp. ? Gnath.
central	(tectum), cerebellum, acusticum, gen. cutaneous nucleus, sp. V tract, nuc. funiculi.																
special cutaneous peripheral central					acustico-lateral system of organs and nerves. cerebellum, acusticum, spinal VIII tract to the nucleus acustici spinalis.												
special sense		later. eyes	1st. epiph.	2nd. epiph.													
SOMATIC MOTOR DIVISION peripheral central			---- nuc. s. m. f.	---- s. m. f.	N. III nuc. III	N. IV nuc. IV	N. VI nuc. VI	[s Fürb.] s. m. f.	[t] s. m. f.	u s. m. f.	v s. m. f.	w s. m. f.	x s. m. f.	y s. m. f.	z s. m. f.	1 sp. Fürb. ventral mot. col.	2 sp. ventral mot. col.
SPLANCHNIC SENS. DIV. *general visceral* peripheral				N. thal. N. cil.			comp't in N.VII shifts to viii	comp't in N. IX shifts to ix	comp't in N. X; shifts to x in Gnath.	comp't col'ct'd into N. X	comp't col'ct'd into N. X	comp't col'ct'd into N. X	comp't col'ct'd into N. X	comp't in r. br.-int. X	comp't in r. br.-int. X	comp't in r. br.-int. X	comp't in r. br.-int.X
central				?				lob. fac.	lob. vagi	lob. vagi	lob. vagi	lob. vagi	lob. vagi	lobus vagi and nucleus commissuralis of Cajal.			
special visceral	The gustatory components and their centers have not been fully distinguished from the general visceral in any vertebrate.																
special sense	N. olf.																
SPLANCHNIC MOTOR DIV. peripheral						mot. N.V shifts to vii	mot. N. VII shifts to viii	mot. N IX shifts to ix	mot. N. X shifts to x Gn.	mot. N. col'ct'd into N.X	mot. N. col'ct'd into N.X	mot. N. col'ct'd into N.X	mot. N. col'ct'd into N.X	N. access.	N. access.	N. access.	N. access.
central						lat. mot. nuc. V	lat. mot. nuc. V	lat. mot. nuc. VII	nuc. IX and X; continued as the lateral motor column of spinal cord.								

nerve root passed behind (caudal to) the myotome of the segment to which it belongs.

c. Various shiftings of organs have taken place, due to (1) the expansion of the branchial apparatus and (2) the formation of a rigid cranium with the consequent loss of dorsal musculature. The shifting which may be observed during the ontogeny is a valuable source of information which should be further studied.

d. Largely on account of the peculiar relations with the ear, the nerve roots connected with the medulla oblongata have shifted backward during the phylogeny, and have left two neuromeres without nerve roots.

e. As a result of the expansion of the branchial apparatus the visceral sensory and motor components of the nerves caudal to the glossopharyngeus have been collected into a common root, the vagus. The somatic sensory and motor components of more or fewer of these nerves are present as rudimentary or complete dorsal and ventral roots which occupy the position of the original nerves. The number of these nerves retained depends upon the reduction of myotomes and cutaneous area in the postauditory region. In cyclostomes all the general cutaneous roots are present and independent; two of the somatic motor roots have disappeared. In gnathostomes, owing to the shifting backward of the vagus root at its attachment to the brain, the general cutaneous root following it has been absorbed and appears in the adult as the second r. auricularis vagi.

f. There has been no shifting forward of spinal nerves into the oblongata.

6. The typical sense organs of vertebrates fall into two categories: the neuromast organs constituting the acustico-lateral system, and the end buds or taste buds. These two sets of organs are absolutely distinct in structure, function, innervation, and central nerve relations.

7. It has previously been shown that the acustico-lateral system was derived from the general cutaneous. It is thought that the neuromast organs appeared first in a marginal portion

of the primitive neural plate. The material used in the formation of these organs was a portion of that part of the neural crest which gave rise to the general cutaneous component. The neuromast area was largest in the region of the VII nerve and neuromere vii, but extended forward probably one or two segments. It can not be exactly compared with the dorsal rami. It is thought that this area, together with the cutaneous ganglion cells, remained outside the neural tube and that later the ganglion cells migrated into the space between the ectoderm and neural tube. This is repeated in the ontogeny in the phenomena of the dorso-lateral placodes and the formation of ganglia from them.

8. The visual organs are thought to have been derived from the neural crest area also, in segments 2, 3 and 4. The retina of the lateral eye is supposed to contain the equivalent of a general cutaneous ganglion and its primary brain center. The optic tract is homologous with the internal arcuate fibers which arise from the cutaneous centers, decussate in the base of the brain and run to the tectum opticum. The epiphyses are thought of as modified general cutaneous ganglia whose centers have remained in the brain.

9. The olfactory organ is regarded as a special collection of sense cells of the invertebrate type, sensitive to chemical stimuli, which are gathered above the hypophysial opening as the organs of the same type in the invertebrate are gathered in the roof of the mouth and on the prostomium.

10. On account of the similarity of their function it is expected that some morphological relation will be found between the olfactory and gustatory organs. The source of the end buds, the origin and history of the nerve components which innervate them, and the course of the gustatory paths in the brain constitute one of the most important problems in vertebrate morphology.

11. It is important that the origin of each of the sensory components in the cranial nerves should be fully worked out in at least a few forms. The cells which enter the ganglia from the neural crest and from the placodes should be traced con-

tinuously until their fate is determined. The cells derived from the neural crest should be distinguished into general cutaneous, general visceral, or others as the result might be.

Naples, October 25, 1904.

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DESCRIPTION OF FIGURES.

Abbreviations.

1, 2, 3, etc.—mesodermic somites of VAN WIJHE.

i, ii, iii, etc.- neuromeres of LOCY.

A - praeoral entoderm connected with the origin of somite 1 and the anterior head cavity.

a–l.—area of the primitive neural plate which gave rise to the acustico-lateral system. Hypothetical.

au. v.—auditory vesicle placode.

b1, b2, etc.—branchial clefts.

B1, B2, etc.—branchial arches.

ch.—notochord.

cil. g.—ciliary ganglion.

e. 1—anterior epiphysis.

e. 2—posterior epiphysis.

h.—hyomandibular cleft.

H—hyoid arch.

hab.—ganglion habenulae.

h. l.—portion of common acustico-lateral placode in selachians which goes to form the head lines.

int. arc.—internal arcuate fibers from cutaneous centers.

L—nerve of LOCY (Fig. 10) and its center (Fig. 7).

l. l.—portion of acustico-lateral placode which forms the lateral line.

m.—mouth.

M—mandibular arch.

mes.—mesoderm.

N. I, II, III, etc.—cranial nerves.

N. olf.—nervus olfactorius.

N. prof.—nervus ophthalmicus profundus.

N. thal.—nervus thalamicus of PLATT.

op. v.—optic vesicle.

s.—striatum.

s. m.—somatic motor column.

sp. m.—splanchnic motor column.

sp. s.—splanchnic sensory column.

s. s.—somatic sensory column.

s. v.—secondary vagus tract.

sy. g.—sympathetic ganglion.

T—hypothetical center for the nervus thalamicus (visceral).

t. b-t.—tractus bulbo-tectalis.

t. l-b.—tractus lobo-bulbaris.

t. t-b.—tractus tecto-bulbaris.

t. t.l.—tractus tecto-lobaris.

t. o.—tractus opticus.

t. o-h.—tractus olfacto-habenularis.

t. s.th.—tractus sacco-thalamicus.

tr. n.—trunk nerve.

An arrow point in Fig. 8 indicates the hypothetical margin of the primitive neural plate; in Fig. 10 indicates the anterior end of the brain.

PLATE I.

Figures 1-7 illustrate the longitudinal zones of the brain and the relation of the brain commissures to them. Fig. 7 is a median sagittal section of the brain of a fish on which are projected the zones of the right half of the brain. The location of the various decussations is also indicated by symbols which are explained on the plate. The places of exit of the nerve roots are indicated by the usual Roman numerals. The lateral line roots arise near to or above VIII. The olfactory centers have been shown in the same shading as the visceral sensory centers in the medulla oblongata. The secondary vagus nucleus and the hypothetical nucleus of the nervus thalamicus are also shown in the same way. The ventro-mesial zone, marked by small circles in this and Fig. 1, is made up of cells which closely surround the mid-ventral furrow of the ventricle. These cells form important nuclei in the inferior lobes, the nucleus thaeniae, corpus interpedunculare and nucleus of MEYNERT's bundle (and possibly the lower olive in fishes). This area corresponds to or includes the Bodenplatte distinguished by His in the embryonic brain. Fig's. 1-6 represent cross sections at the levels indicated by the reference lines. More structures are shown in some of the figures than would appear in an actual section.

Fig. 1.—Section through the superior commissure, ganglia habenulae, thalamic nucleus of the somatic motor fasciculus, and the inferior lobes in front of the saccus vasculosus. The position of several fiber tracts is shown.

Fig. 2.—Through the tectum opticum, dorsal decussation, ansulate commissure, and the nucleus of N. III.

Fig. 3.—Through the cerebellum and the root of N. V. Both somatic and visceral decussations in the cerebellum are shown.

Fig. 4.—Through the root of N. IX. The difference in the course of the secondary tracts from the somatic sensory and the visceral sensory centers is shown.

Fig. 5.—Through the commissura infima HALLERI.

Fig. 6.—Through the root of a spinal nerve and showing the dorsal and ventral decussations of the spinal cord.

Plate I.

Somatic sensory division

Splanchnic sensory division

Splanchnic motor division

Somatic motor division

Splanchnic sensory decussation, first order

Splanchnic sensory decussations, second and third orders

Somatic sensory decussation, second order; posterior commissure

Decuss. tr. tecto-lobaris

Som. sens. dec., internal arcuate fibers; optic tract

Decuss. tr. lobo-bulbaris; ventral commissure

Ventro-mesial zone (Bodenplatte)

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Fig. 8.

Fig. 9.

Plate IV.

Fig. 10

Somatic sensory div.   Splanchnic sensory div.   Splanchnic motor div.   Somatic motor div.

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PLATE II.

Fig. 8, A, B, C.—Three diagrams to illustrate the hypothesis of the origin of the acustico-lateral system from the margin of the neural plate. Each functional division of the nervous system is represented by one cell and fiber. Several general cutaneous ganglion cells which are destined to form the acustico-lateral ganglion are shown. The mesoderm and somatic motor nerve are omitted from *C*, because by the time the acustico-lateral system has reached the grade of development represented, somite 4 no longer forms a myotome.

PLATE III.

Fig. 9, A-G.—Seven outline diagrams to illustrate the hypothesis of the origin of the eye by modification of a general cutaneous ganglion and its corresponding centers. The retinal area is indicated by a row of large dots. The relation of the inner wall of the optic vesicle to the choroid plexus, spoken of in the text, is shown in F and G. A comparison of Fig. 9 F with Fig. 4 will show the similarity of position between the retina and acusticum. It will also show that the optic tract fiber from the retina takes a course corresponding to that of the secondary fiber (internal arcuate) from the cutaneous nucleus.

PLATE IV.

Fig. 10.—A diagram of segmentation in a generalized vertebrate head. In its general features the diagram follows Petromyzon more closely than any other form. So, the number of the gill clefts, their position relative to the somites, the position of the auditory vesicle, and the formation of hypobranchial muscles from myotome 10 and following, are taken from Petromyzon. The neuromeres, the nerve of LOCY, the nervus thalamicus, the relation of the head lines to the auditory vesicle, and the praeoral entoderm are taken from selachians. The sensory nerve roots are represented as retaining their attachment to the dorsal surface of the neural tube where they were formed from the neural crest. The segmental position of these roots is about that which they have in the embryo of Petromyzon, except the root of N. X, which has been shifted back a little farther than it is in Petromyzon. The general cutaneous nerve shown in dotted outline over somite 6 is the Vagusanhang of HATSCHEK in Ammocoetes and the nerve which unites with the vagus root in the embryo of selachians. The position of the viscero-motor nuclei somewhat caudal to the several roots is indicated. The viscero-motor nucleus of the vagus and accessorius is shown as a single large nucleus extending through two segments. It might more properly have been continued caudally until it came into connection with the viscero-motor nucleus of the trunk nerve. The accessorius nerve is not shown. The somatic nucleus and root are shown for all the somites except somite 4, where they are shown in dotted outline. The nerves for both somites 4 and 5 are absent in Petromyzon. Probably both are present in Bdellostoma (α'v and β'v of FÜRBRINGER). It is possible that one or both of these has joined with N. VI in gnathostomes.

LITERARY NOTICES.

Loeb, Jacques. Studies in General Physiology. *Chicago, The University of Chicago Press*, 1905. Part I. xiii + 423, Part II. xi + 425-782.

These volumes contain a series of thirty-eight of the author's papers, all of which are reprinted and most of which originally appeared in German. Within the field of comparative neurology and psychology we note the following papers of the series: "The Heliotropism of Animals and its Identity with the Heliotropism of Plants; Further Investigations on the Heliotropism of Animals and its Identity with the Heliotropism of Plants; On Instinct and Will in Animals; Geotropism in Animals; The Artificial Transformation of Positively Heliotropic Animals into Negatively Heliotropic and *vice versa*; Contributions to the Brain Physiology of Worms; Has the Central Nervous System Any Influence upon the Metamorphosis of Larvae?; On the Theory of Geotropism."

Since the various papers of these volumes received review notice when first published it will suffice, while announcing the fact that they are now available in English, to call attention to the author's scientific life-purpose and the relation which these papers bear to it. From the preface we quote, "a single leading idea permeates all the papers of this collection, namely, that it is possible to get the life-phenomena under our control, and that such a control and nothing else is the aim of biology." According to their method of approach to this goal of research the papers fall into three groups: first, those which are concerned with the control of movement; second, those which deal with the control of regeneration and the determination of organ-formation; third, those which concern the control of the development of the egg.

It is needless to say that Professor LOEB has made great strides toward the accomplishment of his scientific purpose. His work is of great importance; indeed, even when it has followed wrong paths, it has been of value for its stimulating and research-impelling influence. R. M. Y.

Herrick, C. Judson. The Organ and Sense of Taste in Fishes. *U. S. Fish Commission Bulletin* for 1902, pp. 237-272, 1904.

The sense of taste in fishes is subserved by a portion of the communis system of neurones. The sensory organs of this gustatory system are either 'taste buds' situated in the mouth and on the lips, or else terminal buds or end buds (*Endknospen*, *Becherorgane*) situated on the outer surface of the head and body and on the fins. These organs have a general resemblance to one another, and are histologically distinguishable from the neuromasts (*Nervenhügel*) of the lateral-line system. The outer surface of the body is further provided with sense organs of touch having their own distinct innervation. It has been asserted and denied that the end buds or *Becherorgane*, found in the outer skin of the body and fins, serve the sense of taste rather than of touch; but this paper seems to establish conclusively that they are organs of taste.

The proof is as follows. The cat-fish (*Ameiurus nebulosus*) normally makes very little use of its eyes in getting food, but wanders about waving its barblets gently back and forth or trailing them on the bottom, and darting instantly at any game that they happen to touch. The fish darts in just the same way at a piece of meat (on the end of a wire) that is brought in contact with the barblets or any part of the head or body; and the reaction is quite independent of the animal's seeing or not seeing the food. Now if cotton is substituted for the meat, the animal will respond in the same way for five or six times, but will then no longer respond to cotton although it will at once respond again to meat. In other words, after a very brief training Ameiurus responds to taste but not to touch. That the response is really to taste and not to different qualities of touch is proved by the fact that while plain cotton remains unnoticed, cotton soaked in meat juice is snapped up instantly. "These experiments seem to show that in the reaction to meat, both from the barblet and from the skin of the body, the senses of taste and touch both participate. This is in accord with the known innervation of the skin and barblets, for all parts of the body surface receive general cutaneous (tactile) nerves, and all parts are plentifully provided with terminal buds (taste buds) which are innervated by communis (gustatory) nerves." The described reaction does not take place unless the stimulus is actually in contact with the skin, and yet the fish becomes somewhat restless in near proximity to the stimulus, specially if the latter is a piece of meat that has become stale. In order to explain this Professor HERRICK suggests a 'sense of smell', meaning by this a stimulation of sensory

organs in or about the nostrils of the fish, although he himself elsewhere admits in a similar case the possibility of a slight and widely diffused stimulation of end buds on the barblets and body. Further experimentation showed that there are two well defined types of reflex, the gustatory and the tactile.

Similar experiments on three types of gadoids, the pollock (*Pollachius virens*) hake (*Urophycis tenuis*) and tomcod (*Microgadus tomcod*), gave entirely consonant results. In the tomcod the olfactory organs of several individuals were extirpated, but the gustatory reflexes seemed absolutely unmodified by the operation. The sea-robin (*Prionotus carolinus*) finds its food largely by the sense of vision, but also uses not a little its pectoral fin. Now this fin has neither end buds nor communis nerve fibers, and, quite as was to be expected, it shows absolutely no gustatory sensitiveness; the last observation is confirmed by MORRILL. The paper concludes with further interesting observations on the feeding habits of these and other fishes and with interesting general comparative-physiological and comparative-psychological conclusions.   E. B. H.

Carlson, A. J. Further Evidence of the Nervous Origin of the Heart-Beat in Limulus. *Amer. Jour. Physiol.*, 1905, **12,** 471-489.

This is another important contribution, by Dr. CARLSON, to the study of the relation of the nervous system to heart-beat. The author makes clear that nerve elements are demonstrable anatomically as well as physiologically in the hearts of many invertebrates which are generally supposed to lack them.

Among the striking facts in this paper we note : (1) The ganglion cells of the posterior or venous end of the heart of Limulus are more numerous and exhibit greater automatism than those of the anterior end. (2) The nerve cord on the dorsal side of the heart is a reflex centre, but there is no evidence of a local inhibitory reflex mechanism.

(3) Hearts with nerve cord intact vary less in their beating in response to different intensities of stimulation than do those without neural connections. (4) Mechanical stimuli of various kinds produce or augment the rhythmic contractions of the heart with nerve cord, but after extirpation of the ganglion no contractions result from such stimuli.   R. M. Y.

Kendall, W. C. Habits of Some of the Commercial Cat-fishes. *Bull. U. S. Fish Commission for* 1902, 399-409, 1904.

This paper brings together the most important published and otherwise available facts on this subject. Habitat, food, feeding and breeding habits are the chief topics considered.   I. A. FIELD.

THE SENSE OF HEARING IN FROGS.

By Robert M. Yerkes.

From the Harvard Psychological Laboratory.

With Seven Figures.

CONTENTS.

I. Historical Setting of Subject.

1. Hearing in frogs and fishes. The question of the existence of a sense of hearing in frogs is not, as in fishes, an historical problem. For while the question, Do they hear? has been asked repeatedly concerning fishes, and answered as often with 'No' as with 'Yes', students of sense-physiology and animal behavior have assumed, without investigation, that frogs are stimulated by sound. This unquestioning belief in the existence of hearing in frogs is doubtless due to the presence of a prominent ear drum and the ability to produce sounds. Frogs differ from fishes, with respect to the structure of the ear, in that they possess an ear-drum together with a bone which con-

nects it with the ear-sac; and they differ from mammals, to mention only the two chiefly significant features, in that they lack an organ of CORTI and a pinna.   Anatomically the fish and the mammal represent respectively the simplest and most complex conditions in the vertebrate auditory series.   It is not hard to see why investigators should have been interested first and chiefly in the problems of the existence and state of development of the sense of hearing in those vertebrates which have labyrinth organs only (fishes), and in those which have also an organ of CORTI (mammals, for example).   In the case of the former, lacking as they do all external evidence of an auditory organ as well as the organ of CORTI, which is the recognized special organ of hearing in the mammals, it it is not at all surprising that considerable doubt should have existed at various times concerning the existence of a sense which may properly be called hearing. Since frogs stand between fishes and mammals in the vertebrate auditory series, they would naturally be expected to hear in case fishes do.   Attention has long centered where the existence of hearing seemed most doubtful, and it will be profitable for us, before taking up the special evidence of hearing in the frog to note the result of the most recent study of hearing in fishes.

The history of the investigation of the functions of the ear in fishes is a curiously interesting and instructive chapter in the progress of sense-physiology, for it exhibits the development of scientific method, as well as the gradual increase in the scope and exactness of knowledge.   A brief historical sketch of the subject is given by PARKER[1] in a paper on hearing and allied senses in fishes.   In this excellent contribution to the subject the author, after defining hearing "as that sensory activity resulting from a stimulation of the ear by material vibrations" (p. 46), states that Fundulus and several other fishes, which when normal respond definitely to vibrations of a frequency of 128 per second transmitted directly to the water of an aquarium,

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[1] Hearing and Allied Senses in Fishes.   *Bull. U. S. Fish Com.* 1902. pp. 45-64.

fail to respond after the eighth nerves have been cut. The conclusions to which Parker was led by his vivisectional experiments are clearly and briefly stated in his own words, thus:

"The skin, lateral-line organs and ears represent, figuratively speaking, three generations of sense organs. The oldest is the skin stimulated by varying pressures, such as are produced by irregular currents, and capable of initiating equilibration responses. From the skin have been derived the lateral-line organs stimulated by water vibrations of low rate, and also significant for equilibration. Finally, from the lateral-line organs have come the ears stimulated by water vibrations of a high rate and important for equilibration. The ear, unlike the skin and lateral-line organs, is differentiated for its two functions, the sacculus for hearing, the utriculus for equilibration."[1]

In the literature on the senses and reactions of frogs I have found nothing which contributes importantly to our knowledge of the sense of hearing. Most of the investigations which deal with the ear are concerned with the equilibrational and orientational functions of the labyrinth organs and have nothing whatever to say about hearing. In the natural histories the existence of a well-developed sense of hearing is usually assumed, and numerous instances of what are supposed to be reactions to sound are cited. It is to be noted, however, that none of the observations in these popular works furnishes satisfactory proof of the exclusion of the influence of visual stimuli. Among the few references to frog audition of which I have knowledge the only one which seems worthy of special notice is that of Gaupp in his "Anatomie des Frosches." Since his few paragraphs sum up the state of our knowledge on the subject, while at the same time furnishing an illustration of the assumption of hearing on the basis of analogy, I present the substance of them in free and slightly abbreviated translation.

"The labyrinth organ has an acoustic and a non-acoustic (static) function. For these two functions, according to the leading if not generally accepted view, entirely different portions of the organ are in question, and since the non-acoustic is attributed to the three *Cristae acusticae ampullarum* and the three *Maculae* (*M. recessus utriculi, M. sacculi, M. lagenae*) there remain for the acoustic function only the *Papilla basilaris* and the *Macula neglecta*. It is not certain, however, that the non-acoustic organs do not participate in the acoustic function.

"With regard to the acoustic sense of the frog nothing exact is known..

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[1]Abstract of paper read before Section F. of the Amer. Assoc. for the Advancement of Science in Philadelphia, 1904. *Science,* **21,** 265, 1905.

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That it exists, and that in good development, is certain. The existence of the drum and columella, and the fact that frogs have a voice are unmistakable proofs of hearing. The participation of the *Papilla basilaris* in acoustic functions is rendered certain by comparative anatomical studies: the *Papilla basilaris* is the nerve end-organ from which, in the mammalia, the undoubtedly acoustic organ of CORTI arises. From analogy of structure we may also infer an acoustic function in the *Macula neglecta*: on this as on the *Papilla basilaris*, there is a simple tectorial membrane, and further the *Pars neglecta*, like the *Pars basilaris*, has a strong thick wall which only in a limited region, namely, where it approaches a part of the perilymphatic space, is markedly thinner. (For fish BREUER (1891) has already stated that if they really hear—which is not proved—the *Macula neglecta* alone can come into consideration in connection with the function for there is no *Papilla basilaris* in fishes and the six other nerve end-organs apparently serve the non-acoustic function.)

. "In what way the sound waves come to the *Macula neglecta* has already been discussed: it is most probable that the movements of the perilymph, which are produced in the *Spatium sacculare cave perilymphatici* are transmitted to the endolymph of the *Succulus* and that the waves of the endolymph continue from the last directly to the *Pars basilaris* and *Pars neglecta*. The thin walled portions of these two regions would have value as elastic vibratory structures, but they could not serve, as might appear, for the transmission of waves from the perilymph to the endolymph.

"The fact that the vibration of the drum must be transmitted by the plectrum and the *Spatium sacculare cave perilymphatici* first to the *Sacculus* deserves consideration from the point of view of the assumption of a non-acoustic function of the *Sacculus*. It must remain a question whether the movements produced in the endolymph of the *Sacculus* are without effect upon the *Macula sacculi*, perhaps by reason of the very large otoliths, or whether they do not come to perception also at this place (*Macula sacculi*). This same question arises also for the *Lagena*, in which the wave of the endolymph of the *Sacculus* must be continued, as in the *Pars neglecta* and the *Pars basilaris*. It is less probable that the movements may be continued as far as the *Macula recessus utriculi* and the three *Cristae ampullarum*. The question of HENSEN is certainly justified in the case of frogs (1893) "Hier (bei den Fröschen) ist aber schon der acustiche Zuleitungsapparat nicht erheblich viel schlecter als bei den Vögeln entwickelt; sollte das nur zu Gunsten des kaum im Werden begriffen Schnelkenanhangs geschehen sein?"[1]

2. *The ear of the frog.* The anatomical references in GAUPP'S discussion may be made more intelligible by a brief description of the ear. It consists of a large external membrane, the tympanum, usually not more than a centimeter in diameter in the green frog (see Fig. 3), the columella which connects the tympanum with the labyrinth (see Fig. 2), and the

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[1]Anatomie des Frosches. VI. Lehre von Integument und von den Sinnessorganen. S. 751-52. 1904.

labyrinth with its several sense organs. The labyrinth is consti-
tuted by three semicircular canals each of which has a sense-organ,
the *Crista acustica*, in its ampulla, the utriculus, the sacculus and
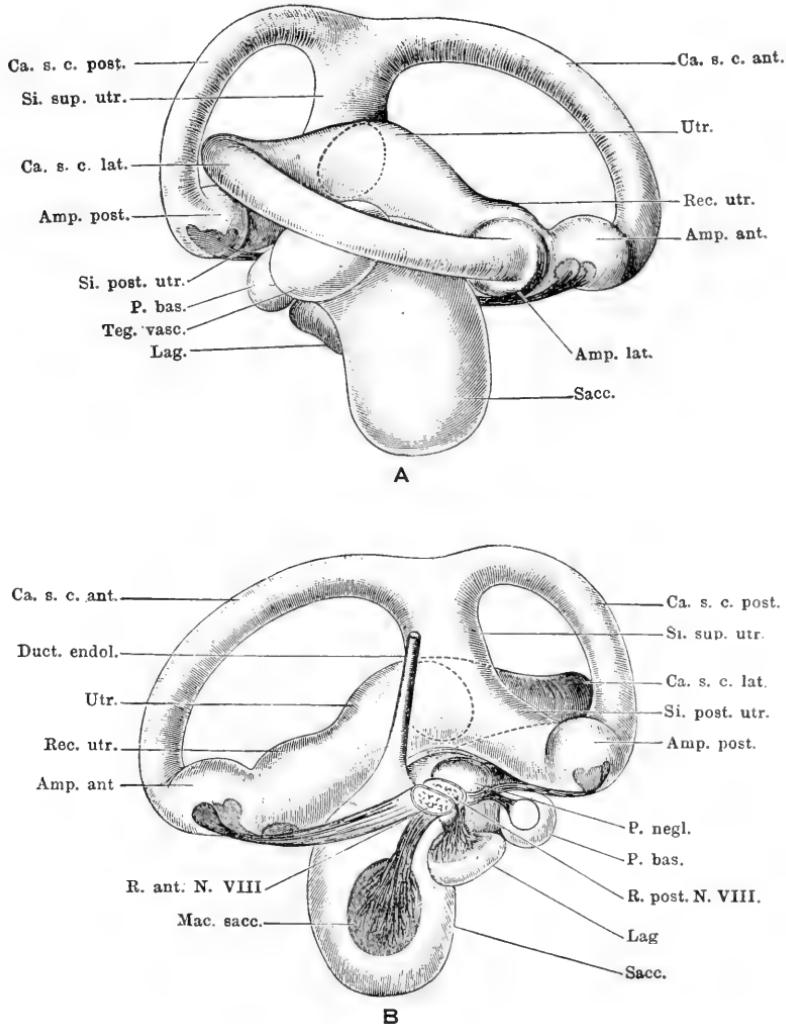
Fig. 1. Membranous labyrinth of *Rana esculenta*, After GAUPP'S modifi-
cation of RETZIUS' drawing ; *A*, seen from the outside ; *B*, seen from the inside.

the lagena, in which together there are five sense organs.
Figure 1, A and B are reproduced from GAUPP'S "Anatomie des

Frosches." Fig. 1 A is a lateral view of the labyrinth organs; Fig. 1 B a median view. These figures together represent clearly the important sensory portions of the ear of the frog. Since there is no organ of CORTI, whatever ability to hear the animals may possess must be due to the functioning of some portion of the membranous labyrinth.

Figure 3 is presented for the purpose of showing the striking difference in the size of the tympanum of male and female green frogs. The individual on the right is a male, that on the left a female. Although these two frogs were of the same length and weight the maximum diameter of the tympanum in
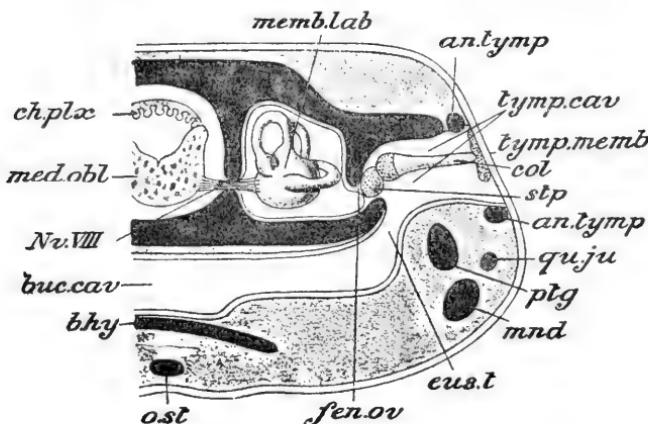
Fig. 2. Transverse section of the head of the frog to show the relations of the various parts of the ear (diagrammatic). *tymp. memb.*, tympanic membrane; *col.*, columella; *stp.*, stapes; *memb. lab.*, membranous labyrinth; *Nv. VIII.*, auditory nerve; *med. obl.*, medulla oblongata; *ch. plx.*, choroid plexus; *tymp. cav.*, tympanic cavity; *fen. ov.*, fenestra ovalis; *buc. cav.*, buccal cavity; *eus. t.*, Eustachian tube; *an. tymp.*, annulus tympanicus; *b. hy.*, body of hyoid; *o. st.*, episternum; *mnd.*, mandible; *ptg.*, pterygoid; *qu. ju.*, quadrato–jugal. From PARKER and HASWELL.

the male is one-third greater than that in the female. Measurements of several other individuals yielded the following results. For ten males whose average length was 7.31 cm. the average maximum diameter of the tympanum was 8.15 mm.; for ten females 6.52 cm. in length it was 5.99 mm. Or if we compare individuals of like size: for a male 6.2 cm. the diameter was 6.3 mm. in contrast with 5.0 mm. for a female of the same

size; in case of two individuals 6.5 cm. the measurement of the male was 7.5 mm., that of the female 6.0 mm.; the tympanum of a male 8.8 cm. long measured 11.5 mm., that of a female 9.0 cm. long, 9 mm. In almost all cases the difference in the size is so marked as to be noticeable to a casual observer.
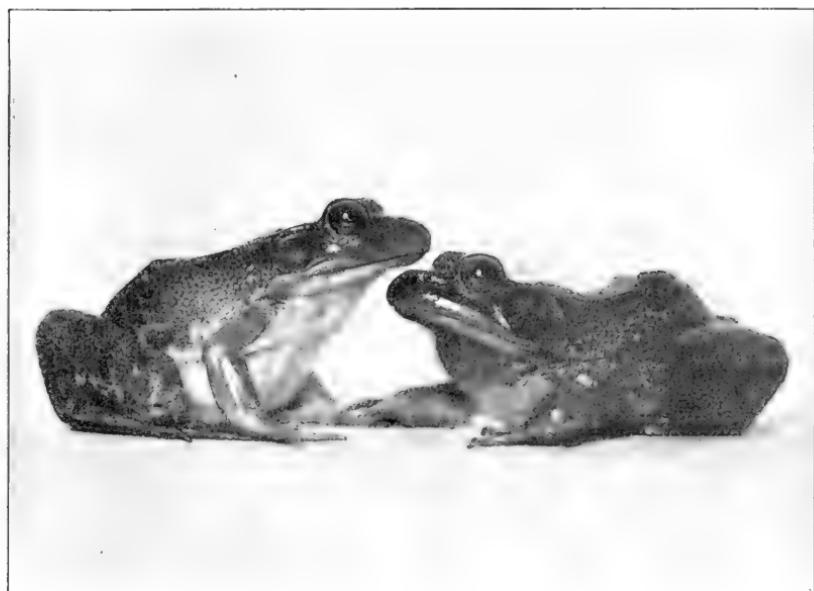
Fig. 3. Photograph of green frogs (*Rana clamitans*), male on the right, female on the left. To show the difference in size of tympana.

3. Problems. The purpose of the investigation of which this paper gives an account was the study of the influence of sounds on the reactions of the frog. The definite questions for which answers were sought are four: 1. Do frogs react to sound? 2. Do they hear? 3. If so, what sounds are heard? 4. Under what conditions do reactions to sounds occur? No attempt was made to localize the function of audition within the labyrinth organs, for the problems of research concern behavior rather than the functions of special organs.

In studies of this sort it is to be remembered that normal behavior can not be studied by vivisectional methods. Oper-

ations on sense-organs, nerve cutting and like methods may aid us in determining what organ or portion of an organ is necessary for a particular function, but they can give us no trustworthy information concerning the relation existing between the senses and the normal behavior of the animal. Therefore, in the experiments now to be described, with the exception of those which were made to ascertain whether the ear is necessary for reaction to sounds, normal frogs were studied either in their native haunts or in the laboratory. All the detailed work was done with the green frog, *Rana clamitans*, but tests were made also with the leopard frog, *R. pipiens*, and the bull frog, *R. catesbiana*.

II. Reactions of Frogs in Nature to Sounds.

My attention was first drawn to the subject of frog audition by failure to obtain motor reactions to sounds in an investigation of the time relations of the neural process of the green frog. Although a large number of sounds of different qualities, pitches and intensities were employed, no visible motor reactions were observed. This led me to seek the significance of what appeared to be either a surprising lack of sensitiveness to changes in the environment which would naturally be expected to stimulate the animal, or an interesting and important case of the inhibition of reaction to auditory stimuli. The question to be answered is, Are frogs deaf, or do they under certain conditions completely inhibit their usual reactions to sound?

Since they bear upon the question of deafness I quote the following observations on the influence of sounds in Nature from the auditory-reaction section of my earlier reaction-time paper.[1]

In order to learn how far fear and artificial conditions were causes of the inhibition of responses to sounds in the laboratory, and how far the phenomenon was indicative of the animal's inability to perceive sounds, I observed frogs in their native haunts.

By approaching a pond quietly, it is easy to get within a few yards of frogs sitting on the banks. In most cases they will not jump until they have evidence

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[1] The Instincts, Habits and Reactions of the Frog. *Harvard Psychological Studies*, **1**, 629-630 (*Psychological Review Monograph*, **4**), 1903.

of being noticed. Repeatedly I have noted that it is never possible to get near to any frogs in the same region after one has jumped in. In this we have additional proof that they hear the splash-sound. To make sure that sight was not responsible for this on-guard condition in which one finds the frogs after one of their number has jumped into the water, I made observations on animals that were hidden from one another. The results were the same. I therefore conclude that the splash of a frog jumping into the water is not only perceived by other frogs in the vicinity, but that it is a peculiarly significant sound for them, since it is indicative of danger, and serves to put them ' on watch.'

A great variety of sounds, ranging in pitch from a low tone in imitation of the bull frog's croak to a shrill whistle, and in loudness from the fall of a pebble to the report of a pistol, were tried for the purpose of testing their effects upon the animals in their natural environment. To no sound have I ever seen a motor response given. One can approach to within a few feet of a green frog or bull frog and make all sorts of noises without causing it to give any signs of uneasiness. Just as soon, however, as a quick movement is made by the observer the animal jumps. I have repeatedly crept up very close to frogs, keeping myself screened from them by bushes or trees, and made various sounds, but have never succeeded in scaring an animal into a motor response so long as I was invisible. Apparently they depend almost entirely upon vision for the avoidance of dangers. Sounds like the splash of a plunging frog or the croak or pain-scream of another member of the species serve as warnings, but the animals do not jump into the water until they see some sign of an unusual or dangerous object. On one occasion I was able to walk to a spot where a large bull frog was sitting by the edge of the water, after the frogs about it had plunged in. This individual, although it seemed on the alert, let me approach close to it. I then saw that the eye turned toward me was injured. The animal sat still, despite the noise I made, simply because it was unable to see me ; as soon as I brought myself within the field of vision of the functional eye the frog was off like a flash.

Many observers have told me that frogs could hear the human voice and that slight sounds made by a passer-by would cause them to stop croaking. In no case, however, have such observers been able to assert that the animals were unaffected by visual stimuli at the same time. I have myself many times noticed the croaking stop as I approached a pond, but could never be certain that none of the frogs had seen me. It is a noteworthy fact that when one frog in a pond begins to croak the others soon join it. Likewise, when one member of such a chorus is frightened and stops the others become silent. This indicates that the cessation of croaking is a sign of danger and is imitated just as is the croaking. There is in this fact conclusive evidence that the animals hear one another, and the probability is very great that they hear a wide range of sounds to which they give no motor reactions, since they do not depend upon sound for escaping their enemies.

The phenomenon of inhibition of movement in response to sounds which we have good reason to think the frogs hear, and to which such an animal as a turtle or bird would react by trying to escape, is thus shown to be common for frogs in nature as well as in the laboratory. This inhibition is in itself not surprising, since many animals habitually escape certain of their enemies by remaining motionless, but it is an interesting phenomenon for the physiologist. We

have to inquire, for instance, what effects sounds which stimulate the auditory organs and cause the animal to become alert, watchful, yet make it remain rigidly motionless, have on the primary organic rhythms of the organism, such as the heart-beat, respiration, and peristalsis. It is also directly in the line of our investigation to inquire how they affect reflex movements, or the reaction time for any other stimulus—what happens to the reaction time for an electrical stimulus, for example, if a loud noise precede or accompany the electrical stimulus.

III. THE INFLUENCE OF SOUNDS ON REACTIONS TO OTHER STIMULI.

1. Influence of sound on respiration and visual reactions.— Observations described in my earlier paper prove that respiration is modified by sounds, and it was also noted that the attempts of a frog to seize a moving object are reinforced by the sound of a tuning fork.[1]

2. Influence of sounds on tactual reactions.—A more detailed study has been made of the influence of sounds on tactual reactions and of the significance of the temporal relations of the stimuli.

A reflex movement of the leg was chosen as an indication of the action of the stimuli and the influence of sounds was observed under the following conditions. A frog was placed on a saddle-like holder and kept in position by linen bands over the back and a wire screen cap over the head, as shown in Fig. 4. Under these conditions the hind legs usually hang free and limp and any movement which may be made by them in response to a stimulus can be read in millimeters from a scale, attached to the holder. This method of measuring the value of stimuli in terms of leg reflex has been used by several other investigators, most recently by MERZBACHER. In this connection it is of interest to note that neither MERZBACHER nor EWALD were able to detect movements of the leg of the frog in response to sounds. Even the croaking of another frog near by had no apparent effect.[2]

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[1] l. c. p. 634.

[2] MERZBACHER, L. Ueber die Beziehungen der Sinnesorgane zur den Reflexbewegungen des Frosches. *Pflüger's Arch.*, **81**, 254, 1900.

I found it desirable, as did MERZBACHER, to observe the movements of a shadow of the leg on the scale and thus read the amount of movement, rather than to watch the leg itself and attempt to project it upon the scale.

As is indicated in the figure the auditory and tactual stimuli were given automatically by means of a swinging pendulum (*P*) which was held in position by the magnet *a* until released by the experimenter. Early in its swing the pendulum turned the key *m* thus completing a circuit which caused the auditory stimulus to be given; later in the swing the key *n* was turned, and the tactual stimulus thus given through the magnetic release of the lever *l*. The interval between the auditory and the tactual stimuli could be varied from .1″ to .9″ by change in the position of the key *n*. For giving the two stimuli simultaneously a double hand key was employed.[1]

The auditory stimulus was either the sound of a quick hammer blow or the ringing of an electric bell for a certain interval. Figure 4 shows the bell. It was placed 80 cm. from the frog, and in order that the influence of vibrations might be avoided was suspended from the pendulum frame. When the hammer was used it was placed 60 cm. from the frog, on the pendulum table. The frog and the apparatus for tactual stimulation occupied a separate table which was not disturbed by the jars of the pendulum table. The tactual stimulus was given by a rubber cone, *T*, Fig. 4, 2 mm. in diameter at its apex. This rubber point, after the electric release of the lever to which it was attached, struck the frog at the middle point of a line drawn between the posterior margins of the tympana. The intensity of the stimulus could be varied by weighting the lever (see *w* in the figure).

Under the conditions of experimentation described above, a tactual stimulus regularly causes a reflex movement of the

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[1] A full account of this method and the results of a study of the phenomena of auditory-tactual reinforcement and inhibition may be found in *Pflüger's Archiv*, Bd. 107, S. 207, 1905, under the title "Bahnung und Hemmung der Reactionen auf tactile Reize durch akustische Reize beim Frosche." In this connection I mention only such aspects of the investigation as bear on the subject of audition.
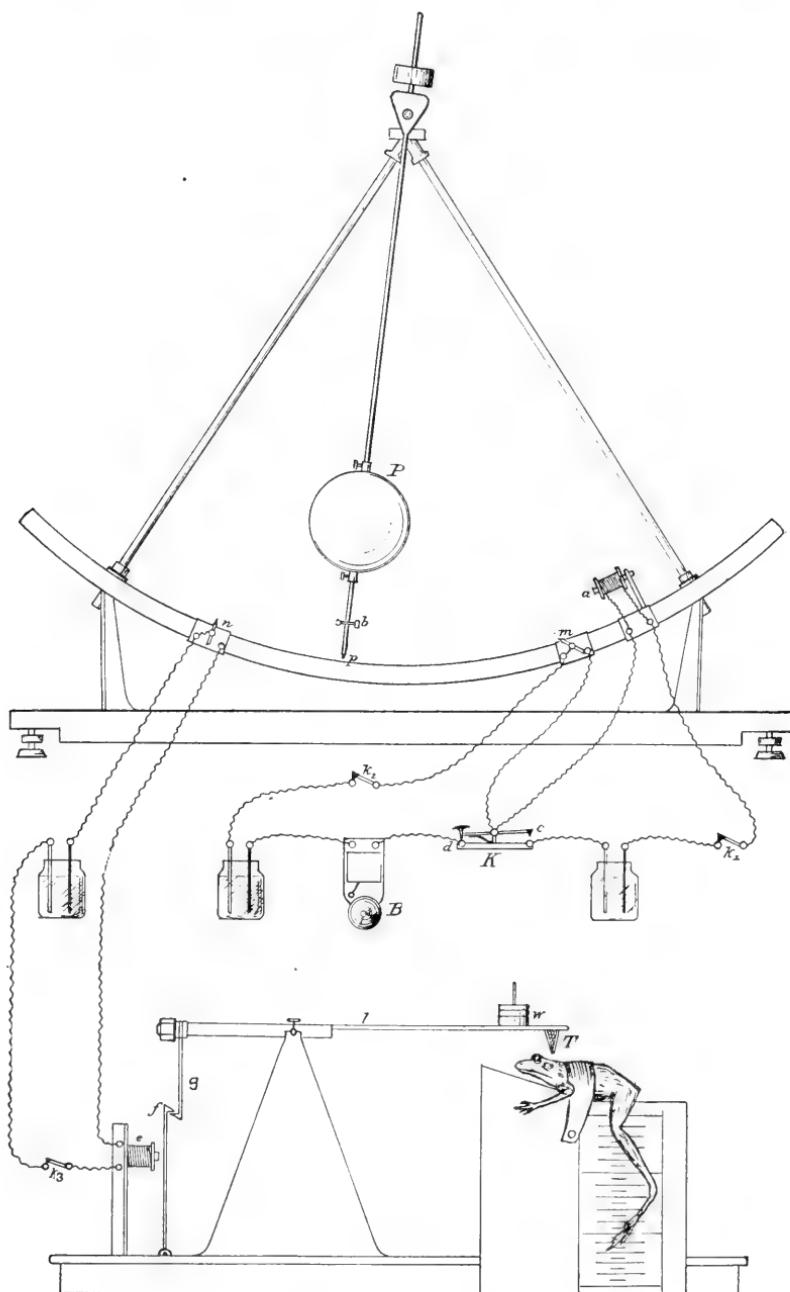
Fig. 4

suspended leg, which varies in amount with the state of the animal and the strength of the stimulus. A sound, on the contrary, never causes the slightest movement, and that no matter how loud or high it be. This makes it possible to study the influence of sounds on tactual reactions, under different temporal relations of the stimuli, for even when the sound precedes the touch there is no reaction until after tactual stimulation.

The results now to be presented were given by the green frog, but test experiments indicate that both the leopard and the bull frog are influenced in similar manner by sounds.

The experimental procedure was as follows. After an animal had been placed in the proper position and had ceased to struggle to escape, reactions to stimuli were taken in pairs regularly at half minute intervals, first a reaction to the tactual stimulus alone, then a reaction to the same intensity of touch when accompanied or preceded by an auditory stimulus.

The series consisted of 50 pairs of reactions taken without pause. So far as the frog is concerned there seems to be nothing undesirable in long series, for there is no indication of fatigue, and so long as the animal is kept moist and in a comfortable position it does not often struggle to escape. The advantage, for the purposes of this investigation, of taking the reactions in pairs is obvious. It permits us to compare directly the reactions of each pair, and to note at once whether the auditory stimulus has reinforced or inhibited the tactual reaction.

During a series the intensity of the tactual stimulus was changed as conditions demanded, but for any one pair of reactions it was always the same. It not unfrequently happened that an intensity which at first caused only slight movement of the leg, later in the series uniformly brought about a maximum contraction, or the reverse might be true, and since the maxi-

Fig. 4. Auditory-tactual apparatus. (Drawn by Dr. WM. E. HOCKING.) *P*, pendulum; *p*, contact point of *P*; *b*, attachment for electro-magnet, *a*; *m*, key for electric bell circuit; *B*, electric bell; *n*, key for magnet circuit of touch apparatus; *K*, hand-key for release of pendulum and temporary closing of electric bell circuit; *k¹*, *k²*, *k³*, keys in circuits; *e*, *f*, *g*, magnetic release for touch apparatus; *l*, pivoted lever bearing rubber cone, *T*, and weights, *w*.

mum amount of movement left no opportunity for judging of the influence of the auditory stimulus it was always necessary in such cases so to alter the intensity of the tactual stimulus that a medium reaction would result.

The animals seldom struggled during experiments, but if too firmly bound they became irresponsive to the stimuli.[1] It was therefore necessary to place them carefully in position, and then, after they had ceased to struggle, to draw the linen bands over them just tightly enough to prevent change in position. For the purpose of excluding the influence of visual stimuli a wire screen cap covered with black cloth was put over the head. This served to help keep the frog in the proper position as well as to exclude visual stimulation.

TABLE I.

THE INFLUENCE OF SOUND ON THE TACTUAL REACTIONS OF THE GREEN FROG.

Green frog A.	*Tactual Stimulus Alone*			*Auditory and Tactual Stimuli*		
	Position of shadow on scale		Amount of movement	Position of shadow on scale		Amount of movement
No. of Exp.	before	after		before	after	
	the stimulus			the stimulus		
Pair 1	10	52	42mm	10	90 M*	80mm.
" 2	15	28	13	20	90 M	70
" 3	15	29	14	15	90 M	75
" 4	15	19	4	15	90 M	75
" 5	10	20	10	10	20	10
" 6	20	27	7	20	90 M	70
" 7	25	40	15	25	50	25
" 8	30	32	2	30	49	19
" 9	30	33	3	Struggle	—	—
" 10	25	31	6	2	46	21
Green frog B						
Pair 1	20	23	3	20	90 M	70
" 2	20	25	5	20	90 M	70
" 3	20	24	4	20	90 M	70
" 4	20	23	3	20	90 M	70
" 5	20	23	3	20	90 M	70
" 6	20	35	15	20	60	40
" 7	20	21	1	20	90 M	70
" 8	20	21	1	20	90 M	70
" 9	20	22	2	20	90 M	70
" 10	20	21	1	20	90 M	70

*M indicates maximum movement of leg.

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[1] A case of inhibition.

The two series of reactions of Table I, chosen at random from several hundred, will serve to indicate the method of recording the results as well as the nature of the results themselves. The first ten pairs of reactions fairly represent the variableness of the reactions; the second show still more clearly the influence of the auditory stimulus.

The results obtained with four frogs, two males (Nos. 1 and 3) and two females (Nos. 2 and 4) will suffice to indicate the influence of sounds on tactual reactions. For each of the four frogs fifty pairs of reactions were taken in series, and that for each of seven different temporal relations of the two stimuli. The individual averages therefore are based upon fifty reactions, and the total number of reactions for each individual is seven hundred. As is clear from column one of Table II, the temporal relations of the stimuli ranged from simultaneity to .9″ (i. e., the auditory preceded the tactual by .9″).

The influence of the sound, which for these experiments was a sudden hammer blow, is discovered by direct comparison of the tactual reaction of each pair with its corresponding auditory-tactual reaction. When the tactual reaction is the greater, we infer that the sound has partially inhibited reaction; when it is the smaller, that it has reinforced reaction; when the two are equal, that it has been without influence. The influence of sound may be expressed either in terms of the number of reactions reinforced, inhibited and equal, or in terms of the amount of reinforcement or inhibition. Both methods have been employed. Table II presents the percentage value of the auditory-tactual reactions in comparison with the tactual, and also the number of reactions over half which were reinforced or inhibited, while Figures 5 and 6 graphically represent the amount of influence in terms of the tactual reaction. The auditory-tactual reaction is always expressed as so many per cent greater (+ i. e., reinforcement) or less (— i. e., inhibition) than the tactual. In the table + always indicates reinforcement, — inhibition, and in the curves the portions above the zero line indicate reinforcement, those below it inhibition. The number of reactions over half, that is over twenty five, since there were

fifty pairs of reaction for each interval and each animal, which were reinforced or inhibited furnishes an excellent quantity for comparison with the averages. As such comparison reveals close agreement between amount of influence of the auditory stimulus and the number of reactions either reinforced or inhibited it is clear that the averages are trustworthy, even though the variability of the reactions is enormous.

TABLE II.

INFLUENCE OF SOUND ON THE TACTUAL REACTIONS OF THE GREEN FROG FOR DIFFERENT TEMPORAL RELATIONS OF THE STIMULI.

Length of interval	Diff. in per cent. between tactual and auditory-tactual reactions	Number of reactions reinforced or inhibited	Diff. in per cent. between the tactual and auditory tactual reactions	Number of reactions reinforced or inhibited
	Male No. 1.		Male No. 3.	
0″	+ 62.0 %	+ 17.0	+ 103.1 %	+ 18.0
.15″	+ 30.3	+ 17.0	+ 85.9	+ 17.0
.25″	+ 33.3	+ 13.0	+ 31.3	+ 12.5
.35″	+ 1.7	+ 0.5	+ 6.4	+ 2.0
.45″	− 22.3	− 10.0	− 4.8	− 4.5
.65″	− 10.0	− 6.0	− 15.0	− 6.5
.90″	+ 0.7	+ 0.5	− 2.1	− 2.5
	Female No. 2		Female No. 4.	
0″	+ 60.9 %	+ 14.5	+ 40.7 %	+ 11.0
.15″	+ 19.8	+ 6.5	+ 31.1	+ 10.5
.25″	+ 30.4	+ 12.0	+ 49.2	+ 13.5
.35″	− 6.3	− 3.0	− 13.2	− 3.5
.45″	− 8.1	− 3.5	− 19.8	− 11.0
.65″	− 15.8	− 9.5	− 7.8	− 5.5
.90″	− 0.9	+ 3.0	− 5.1	− 4.0

The results tabulated in Table II show that the sound when occurring simultaneously with the tactual stimulus greatly increases the amount of the reflex, while on the contrary it decreases the amount of reaction if it precedes the tactual stimulus by .5 to 1.0″. Number 1, for example, exhibited reinforcement equal to 62 % of the amount of the tactual reaction when the stimuli were given simultaneously, but when the sound occurred .65″ before the touch the resulting reaction was 10 % less than the tactual.

In Figures 5 and 6 are curves, representing the amount of reinforcement and inhibition for the four frogs, constructed

according to the following method. Let the zero point on the ordinates represent the value of the tactual reactions; then the value of the auditory-tactual may be indicated on the same ordinate as so many per cent. greater (above the zero point) or less (below the zero point) than the tactual. In Fig. 5, for instance, the sound when simultaneous with the touch caused a
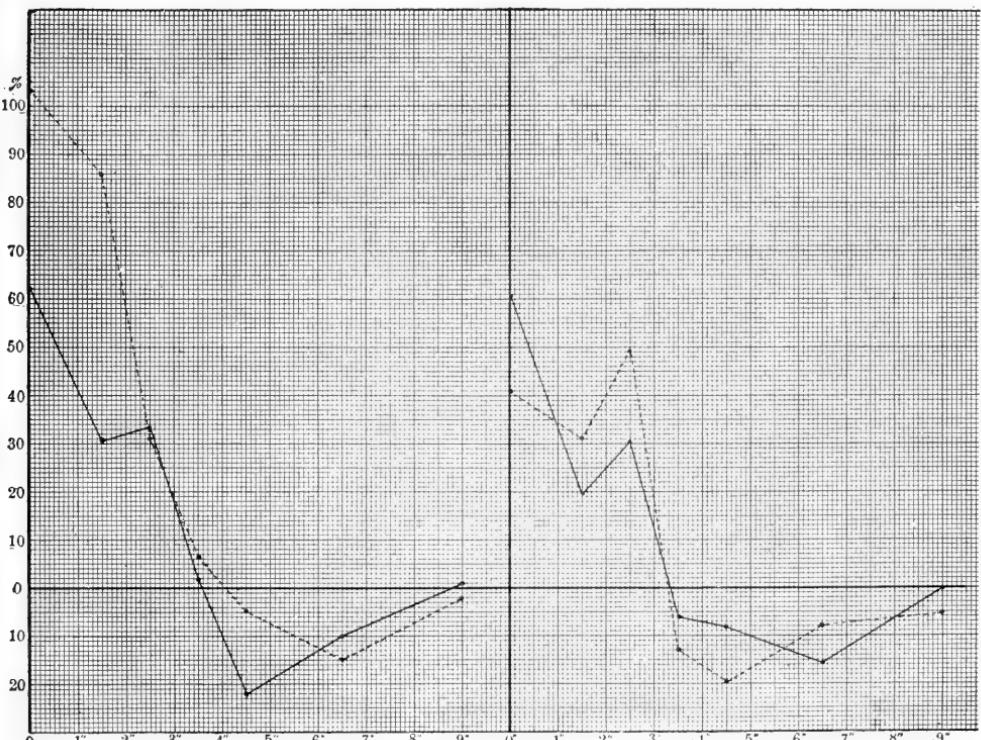
Fig. 5   Fig. 6

Fig. 5. Reinforcement-inhibition curve for momentary auditory stimulation, contructed on the basis of amount of reaction. —————Curve for male No. 1 ; _____Curve for Male No. 3.

Fig. 6. Reinforcement-inhibition curve for momentary auditory stimulation, constructed on the basis of amount of reaction.—— ——Curve for Female No. 2._____Curve for Female No. 4.[1]

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[1]The curve for No. 4, Fig. 6, as originally published in *Pflüger's Archiv*, Bd. 107, S. 219, is incorrect in that it starts with 50.7 % instead of with 40.7 %.

reaction 62 % greater than the tactual, in the case of one frog, and 103.1 % greater in the case of the other. On the other hand, when the sound preceded the touch by .45″ the resulting auditory-tactual reaction was 22.3 % and 4.8 %, less, respectively, than the tactual.

The figures on the left margin of the curves above the zero point indicate reinforcement in per cent. of the tactual reaction, those below the zero point, inhibition. Below the base line the time intervals are given in tenths of a second. Each curve is plotted, from the data of Table II, on the basis of seven hundred reactions. It is to be noted that the curves of Figure 5, for the two males, show considerably more reinforcement than those for the females in Figure 6. Furthermore, the curves for the females cross the transition line between reinforcement and inhibition sooner and return to it more slowly than do those for the males. In other words, inhibition begins with a shorter interval between the stimuli and continues longer.

These experiments prove conclusively that sounds, although they do not call forth the reflex movement under consideration, modify in important ways the action of other stimuli. It is therefore certain that lack of auditory reaction is due to some form of inhibition and not to insensitiveness.

IV. Hearing of Frogs in Air and in Water.

It has· been held by many investigators of the sense of hearing that sounds in the air cannot be heard by animals under water for the simple reason that the air waves cause only very slight disturbances in the water. In view of this statement it is of interest to test the ability of the frog to hear when the tympanum is exposed to air and when it is under water.

Experiments were made with the apparatus represented in Fig. 7. The reflex reaction method of testing the influence of sounds was again employed, and pairs of reactions were recorded for frogs whose ears were either exposed to air waves or submerged in the water of the aquarium. The level of the water, with reference to the ear, was controlled by changing the volume in the aquarium, and the leg of the frog was kept from

floating upward by the attachment of a one gram weight. The two stimuli were given by means of the hand key, *K*. In all cases the auditory stimulus was the sound of an electric bell, *B*, suspended above the water in such a way that its vibrations could not be transmitted either to the aquarium or the frog holder. Precautions were taken to exclude also the influence of visual stimuli.

During the month of December, 1904, ten green frogs were tested with this apparatus and it was found, contrary to the expectations aroused by previous results, that the females
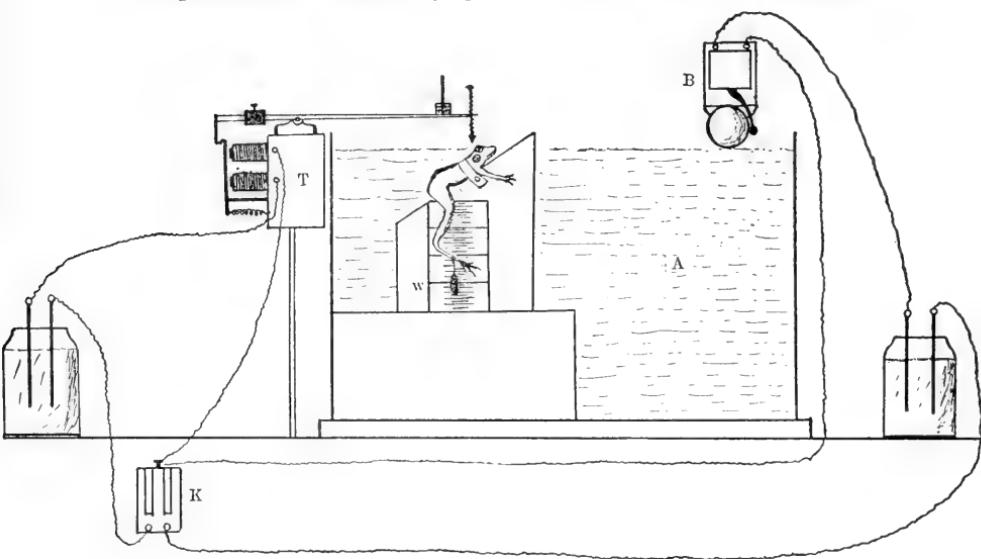
Fig. 7. Auditory apparatus for testing hearing in air and in water. *A*, aquarium ; *B*, electric bell ; *T*, tactual stimulus apparatus ; *K*, hand-key for giving stimuli ; *w*, weight to hold leg.

reacted far more uniformly and vigorously to sounds than the males. Indeed the irregularity of response and irresponsiveness of the males were so marked that it was seldom possible to get more than two or three pairs of reactions in series. For this reason it has been impossible to present averages for the males. The females reacted with a fair degree of regularity, but with notning like the vigor and uniformity which characterized the reactions of animals tested in April and May. Evi-

dently the seasonal condition of the animal is an important matter to consider in studies of audition.

The experiments included tests under three conditions: I. When the tympanum was exposed fully to air, although the body was submerged up to the level of the ear drum ; 2. When the tympanum was half under water, the head and nares being in air ; 3. When the frog was submerged to a depth of 4 cm.

The results prove beyond doubt that sounds made in the air stimulate frogs when their tympana are under water. Furthermore, there is evidence that sounds stimulate the green frog even when it is totally submerged to a depth of four centimeters. I cannot better describe these results than by giving the sample series of Table III.

Although the amount of reaction under the conditions of these experiments is small, the difference between the tactual and the auditory-tactual is sufficiently great to establish the frog's ability to hear under water.

The averages for ten reactions of another female under four sets of external conditions follow :

Condition	Amount of reaction to tactual stimulus alone.	Amount of reaction to the auditory-tactual alone.
Tympanum in air	2.0 mm.	16.4 mm.
" half under water	.9 "	12.5 "
" 1 cm. under water	1.3 "	3.5 "
" 4 cm. under water	.5 "	1.2 "

With several other individuals reactions were obtained which just as clearly indicated audition under water. We may therefore conclude that the green frog can hear both in air and under water.

There is some evidence that the reaction to sound is greatest when the tympanum is half submerged.

V. The Range of Hearing.

By one or another of the methods of experimentation already described the value of the following sounds as auditory stimuli for the frog has been demonstrated during the course of this investigation. The croaking of green, leopard and bullfrogs ; splashing of water ; pistol explosions ; tuning forks rang-

TABLE III.

HEARING OF GREEN FROG IN AIR AND UNDER WATER.

Female. Dec. 5, 1904.
Weight for tactual stimulus 5 grams.

No. of pair (Continuous series)	Tactual stimulus alone			Auditory and tactual stimuli		
	Position of shadow on scale		Amount of movement	Position on shadow on scale		Amount of movement
	before	after		before	after	
	the stimulus			the stimuli		
Series I. Tympanum exposed to air.						
1	28	30	2 mm.	27	50	23 mm.
2	27	30	3	26	30	4
3	26	29	3	26	29	3
4	25	27	2	25	28	3
Series II. Tympanum entirely under water.						
5	25	25	0	25	32	7
6	25	27	2	25	28	3
7	25	28	3	25	28	3
8	19	19	0	19	21	2
Series III. Tympanum half under water.						
9	19	20	1	19	22	3
10	19	19	0	19	22	3
11	19	20	1	19	25	6
12	19	21	2	19	21	2
Series IV. Frog submerged to depth of 4 cm.						
13	19	20	1	19	22	3
14	19	20	1	19	21	2
15	18	18	0	18	20	2
16	18	19	1	18	20	2
Series V. Tympanum exposed to air as in Series I.						
17	18	20	2	18	21	3
81	18	19	1	18	21	3
19	18	20	2	18	22	4
20	18	20	2	18	25	7

ing from 100 to 1000 vibrations per second; electric bell with metal gong and also with wooden gong; sudden hammer blow; Galton whistle; Appunn whistle, and a variety of sounds produced by the human vocal organs.

The sound of the electric bell produces the most marked modification of reaction, probably because it consists, like the induced electric shock, of a rapid succession of stimulating

changes. The green frog is stimulated by sounds as low as 50 vibrations per second. No experimental tests were made with lower sounds. For the purpose of determining the upper limit of audibleness tests were made with Galton and Appunn whistles. The tactual reflex was again employed as a means of testing the influence of sound. The tests, like those of the previous section of the paper, were made during the winter and responses to both tactual and auditory stimuli were obtained much more regularly with females than with males. A sufficient number of reactions have been recorded for males, however, to prove that they are influenced by sounds as high as 10,000 vibrations per second, as are the females also. The following series of averages for a female is indicative of the nature of the results of these tests :

Green frog female	*Galton whistle vibration rate*	*Amount of tactual reaction Average of twenty reactions*	*Amount of auditory-tactual reaction in each case.*
Series I.	5,000	2.80 mm.	4.65 mm.
" II	8,000	2.60 "	5.45 "
" III	10,000	2.10 "	4.20 "
" IV	Puff of air alone	2.45 "	2.30 "

Series IV serves as a control on the influence of the sound of escaping air which accompanies the tone of the whistle. Its result indicates that the tone is the effective stimulus in the preceding series.

Similar results obtained by the use of the Appunn whistles prove that up to 10,000 vibrations per second the frog is stimulated by sound. With neither the Galton nor the Appunn whistles was evidence of reaction to sounds of higher vibration rate obtained. We may therefore conclude, until further investigation by more satisfactory methods is available, that the green frog is influenced by sounds ranging in rate of vibration from 50 to 10,000 per second. It should be noted, however, that neither the upper nor the lower limit of audition has been accurately determined by these experiments.

VI. THE RELATION OF THE EAR TO REACTION TO SOUND.

Abundant evidence has now been presented in support of the statement that the frog is stimulated by sound, but the use of the term audition in connection with these reactions has not been justified. If the investigation were dropped at this point the criticism would doubtless be made that the modifications of tactual reactions produced by sounds may be due to stimulation of certain cutaneous sense organs instead of the organs of the ear, and that therefore nothing has been proved concerning hearing in the frog. In anticipation of this objection to the conclusions which have been drawn from the results of experimentation check observations were made on frogs whose ears had been operated upon in various ways.[1]

The operations whose effects serve as evidence of the relation of the ear to the responses to sounds which we are now considering were three : (1) Cutting the tympana ; (2) Cutting the columellae as well as the tympana ; (3) Cutting the eighth nerves from the dorsal side.[2]

Briefly stated, the results of the three operations mentioned are as follows.

1. After cutting of the tympana there is no apparent change in the nature of the influence of sounds. The frogs are at times less responsive to stimuli, and as a rule they do not show as marked reactions to either touch or sound as do the normal animals.

2. Sounds continue to modify tactual reactions after both columellae and tympana are cut. In one case it was noticed that the influence of the sound of a wooden gong was much increased by this operation, whereas there was no marked change in the influence of the sound of the metal gong. There

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[1]Through the kindness of Mr. J. H. MASON, graduate student in the department of zoölogy of Harvard University, I was enabled to make the following tests on frogs which he had operated upon for the purpose of studying the static functions of the labyrinth organs.

[2]Postmortem examination in case of attempted cutting of the nerves showed in most cases that the ear or brain had been injured. In only two instances was the operation sufficiently clean to fulfill the requirements of the experiments.

is an observation which suggests the importance of the relation of vibration rate to the nature and condition of the transmitting structures. Many individuals failed to react to any moderately intense stimuli within a period of several hours after this operation. The sample series of reactions recorded in Table IV is sufficient comment upon the conclusiveness of the experiments so far as the value of these transmitting organs for so-called auditory reaction is in question.

TABLE IV.

THE INFLUENCE OF SOUNDS ON FROGS WITHOUT COLUMELLAE OR TYMPANA.

Green Frog. Operated April 17, 1904. Reactions taken immediately after operation.

No. of pair	Tactual stimulus alone			Auditory and tactual stimuli.		
	Position of shadow on scale		Amount of movement	Position of shadow on scale		Amount of movement
	before	after		before	after	
	the stimulus			the stimuli		
1	41	41	0 mm.	41	45	4 mm.
2	20	27	7	20	90 M	70
3	15	28	13	15	90 M	75
4	20	20	0	18	25	7
5	25	30	5	15	90 M	75
6	20	90M	70	20	40	20
7	20	35	15	20	90 M	70
8	30	50	20	35	70	35
9	25	33	8	25	35	10
10	25	27	2	25	27	2
	Average for series		14.0 mm.			36.8 mm.

3. After the cutting of the eighth nerves reactions to sounds were not obtained. Tests were made with green frogs and bull frogs, but only with the latter could reactions to tactual stimuli sufficiently great for the purposes of the investigation be obtained after the operation. Of fifteen frogs used only four reacted regularly to tactual stimuli after being operated, and these gave no sign of reaction to sounds. Typical of the results for those individuals which continued to be responsive to tactual stimuli after the operation is the following series, Table V. The eighth nerves of the bull frog used in the experiments of this series were cut May 17; two days later a series of twenty five pairs of reactions was obtained. Experiments were continued at intervals until June 14. The animal was apparently in good condition, the skin wound had healed by the latter date, but auditory reactions were wholly lacking.

TABLE V.

The Influence of Sounds on Frog with Eighth Nerves Cut.

	Bull Frog Operated May 17, 1904.		
Date of series	Amount of reaction to tactual stimulus	Amount of reaction to auditory and tactual stimuli	Number of reactions greater (+) less (—) equal (=)
	Each result is the average for 25 reactions		
May 19	4.16 mm.	4.04 mm.	9 +, 11 —, 5 =.
May 20	19.24	18.20	9 +, 14 —, 2 =.
May 21	15.04	14.28	10 +, 10 —, 5 =.
May 24	13.08	13.28	10 +, 6 —, 9 =.
June 14	8.60	8.76	7 +, 12 —, 6 =.
Averages	12.02	11.71	9 +, 10.6 —, 5.4=.

Cutting of the eighth nerves renders the frog irresponsive to sounds which markedly influence the tactual reactions of the normal animal. We may therefore conclude that the reactions with which we have dealt in this investigation are due to stimulation of certain sense organs of the ear, and that the use of the word hearing in connection with them is appropriate.

VII. Summary and Conclusions.

1. Observation of frogs in their natural habitat shows that they are stimulated by sounds. The sense of hearing apparently serves rather as a warning sense which modifies reactions to other simultaneous or succeeding stimuli than as a control for definite auditory motor reactions.

2. Experimental tests prove that sounds modify the frog's reactions to visual and tactual stimuli. When the sound accompanies the visual or tactual stimulus it serves to reinforce the visual or tactual reaction, but when given alone it never causes a motor reaction.

3. The sound of an electric bell occurring simultaneously with a tactual stimulus markedly increases (reinforces) the leg reflex of green-, leopard- and bull-frogs. If the sound precedes the touch by 1″ it is without effect on the reaction; if the interval is not longer than .35″ it usually causes reinforcement, whereas for an interval of from .4″ to .9″ there is partial inhibition of reaction. According to its temporal relation to

another stimulus, an auditory stimulus may either reinforce or inhibit the reaction appropriate to that stimulus. What may be called reinforcement-inhibition curves for auditory stimuli are presented in this paper.

4. The green frog responds to sounds made in the air whether the tympana be in the air or in water. There is some evidence that the influence of auditory stimuli is most marked when the drum is half submerged in water. The influence of sounds upon tactual reactions is evident when the frog is submerged in water to a depth of 4 cm.

5. Sounds varying in pitch from those of 50 to 10,000 vibrations per second effect the frog. The most striking results were obtained by the use of an electric bell with a metal gong. With this sound in connection with a weak tactual stimulus a maximum reaction of the leg may often be obtained even when either stimulus alone causes no perceivable reaction.

6. Sounds modify the reactions of the frog after tympana and columellae are removed. Cutting of the eighth cranial nerves causes disappearance of the influence of sound. It is clear then that the reactions to sounds are really auditory reactions and that the sense of hearing in the frog is fairly well developed, although there is little evidence of such a sense in the motor reactions of the animal.

7. Those portions of this investigation which were carried out in the spring months show marked influence of sounds for both males and females, whereas experiments made during the winter indicate a much diminished sensitiveness to auditory stimuli in both sexes, but especially in the male.

THE REACTIONS OF RANATRA TO LIGHT.

By S. J. Holmes.

CONTENTS.

I. Introdtction.

In endeavoring to ascertain the way in which animals of various kinds orient themselves to the rays of light I have experimented with quite a large number of species in the hope of finding forms in which the exact mode of response would reveal itself. Animals vary greatly as regards both the definiteness of their reactions to light and the ease with which their movements can be followed. Among creatures of small size such as the Copepoda, Cladocera and Ostracoda, it is almost impossible

to observe the precise movements concerned in orientation, and in many larger forms the rapidity, irregularity, or indefiniteness of their light reactions renders the same difficulty almost equally great. In studying the reactions of animals to light we are naturally confronted with the question as to how far the movements involved are the result of choice, or something analogous thereto, and how far they may be explained as the result of reflex responses to photic stimuli. If they mainly fall into the latter category we are led to inquire just what these reflexes are and how they produce the particular kind of behavior observed.

It is a quite commonly accepted hypothesis that the phototactic reactions of organisms are effected by the action of light directly or indirectly upon the tension of muscles concerned in locomotion. In nearly all insects and in a large proportion of other arthropods this tension, if it exists, must be brought about through the central nervous system, since the opacity of the integument prevents any appreciable direct effect of light upon the musculature. In most arthropods phototactic impulses are set up by means of light entering the eyes, and not as in many lower forms through the stimulation of the integumental nerves ; this is shown by the fact that when the eyes are blackened over or destroyed responses to light no longer occur. In most animals it is not possible to observe any effect of light upon muscular tension, although there is considerable indirect evidence that such an effect is produced. As RADL[1] has remarked, it is difficult to explain the fact that an insect with one eye blackened over moves about in a circle except on the assumption that light affects unequally the tension of the muscles on the two sides of the body. Such circus movements are comparable to those which take place in a vertebrate animal upon the destruction of the semicircular canals in one side of the head. After this operation there is produced a marked difference in the muscular tonus of the two sides of the body and, as a consequence, the animal, instead of going in a normal manner

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[1] Untersuchungen über den Phototropismus der Tiere, 1903.

veers continually toward the weaker side. A small difference in the muscular tension of the two sides of an insect body which would be sufficient to cause the creature to orient itself to the rays of light might not be patent to direct observation, especially if the movements are rapid or irregular, as they frequently are. There are several forms, however, in which the effect of light upon the muscular tone is quite clearly manifested, but none more so than in the common water scorpion, *Ranatra fusca*. In many ways this species is admirably adapted for the study of phototaxis; it is of large size, its long slender legs move in a slow and deliberate manner so that one can observe just how each action is performed; it may be readily kept for a long time in the laboratory, shows no signs of fear when being experimented with, and reacts to light with a remarkable degree of precision. For an investigation of the *modus operandi* of the phototactic response Ranatra is probably not equalled by any other known form.

It is especially advantageous to study phototaxis in some such organism if we wish to ascertain how far the reflex theory of orientation will carry us. If orientation is the result of comparatively direct reflexes we are better able to determine their precise mode of action. If a more involved type of reaction occurs there is a better opportunity afforded for proving its existence, and, perhaps, ascertaining something of its nature. It does not follow that because we can construct a theory to account for orientation by means of direct reflexes that the process necessarily takes place in so simple a manner. Between the stimulus and the reaction there may be processes of a complicated nature whose existence is not ordinarily betrayed by any outward and visible sign. No one would consider a dog's following the scent of a rabbit a matter of simple chemotaxis. While it is not a process requiring conscious ratiocination, it is doubtless one involving psychic operation of considerable complexity. The possibility should be borne in mind that many of the tropisms of insects may be less simple and direct reactions than is commonly supposed. If a bee finds its way to its hive over miles of woods and fields guided by its memories of

the various objects that come into its field of vision, it is certainly something more than a mere reflex machine. In organisms which are capable of a higher type of response we should at least be on our guard in attempting to explain their tropisms as due entirely to direct reflexes involuntarily performed in response to outer stimuli. The conduct of higher animals is guided in large measure by their likes and dislikes, however we may interpret this kind of behavior in physiological terms. Between such behavior and those tropisms which are the result of comparatively simple reflexes there are, no doubt, numerous intermediate kinds of conduct. It is not unreasonable to suppose that tropisms which in low forms are brought about by direct reflexes may in higher animals complicate into reactions of the pleasure-pain type while still preserving outwardly the appearance of a more mechanical mode of response. At the same time an element of direct reflex action may be retained, although closely associated with and capable of being modified by more complicated neural processes. A consideration of the experiments described in this paper will lead us, I think, to some such view.

II. General Habits.

Ranatras are generally found in ponds or streams among masses of vegetation where they lie quiet the greater part of the time. Although capable under certain conditions of manifesting considerable activity, these insects are usually sluggish in their movements. Their choice of habitat is probably determined, in great part at least, by their positive thigmotaxis, since they tend to insinuate themselves between objects which afford considerable contact stimuli. Their habit of coming together to form groups is a manifestation of the same tendency. When several individuals are placed in an aquarium they mass together when at rest to form a cluster in which they are often so closely aggregated and so tangled together that those which are near the center of the group experience much difficulty in disengaging themselves. In this way they may lie for n an almost motionless state.

The general form and dull coloration of Ranatra tend to make it inconspicuous in its natural habitat, especially as it does not reveal its presence by its movements. When lying in the water the long breathing tube through which air is admitted to the body rests at the surface. The two parts of which it is composed occasionally approach and recede from each other, moving the air between them to and fro, an operation which doubtless assists in respiration. Air is prevented from escaping when the valves are separated, by the rows of hairs which line the margins of the concave inner faces of these structures.

Ranatra is carnivorous in habit, seizing its prey with its anterior raptorial limbs and holding it until it has sucked out its juices. It is quite destructive of fish eggs and frequently attacks and sucks the blood from young fishes. It is also reported to prey upon young tadpoles. De la Torre Bueno[1] describes the method Ranatra employs in capturing prey as follows: "When a fly attracts its attention Ranatra very slowly, almost imperceptibly, moves its fore legs, with the knife-like tarsus away from the tibia, towards its prey. When the tibiae are almost, or quite, touching the victim the movement is so sudden and quick that one is aware of it only by seeing the prey seized. Sometimes its hold is not satisfactory, and then it will let go with one tarsus, get a firmer grip with that, and then do the same with the other. Once it has the fly securely held, Ranatra slowly approaches it to its extended beak, with which it seems to touch and feel until it finds a suitable spot, and proceeds to a leisurely meal." I have usually fed Ranatras during the winter on *Notonectas*, or back-swimmers, as these insects were easily obtained during this time of year. The Ranatras did not pursue the back-swimmers, but as soon as their attention was attracted to the prey they lay quietly in readiness for them with their anterior limbs prepared to quickly seize the small insects should they swim sufficiently near. If a *Notonecta* strikes against a Ranatra the latter makes a quick

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[1]Notes on the Stridulation and Habits of *Ranatra fusca* Pal. B., *Canadian Entomologist*, Vol. 35, p. 235, 1903.

grab for it, and, if successful in seizing it, proceeds to suck out its blood in the manner described by DE LA TORRO BUENO.

In locomotion, either by swimming or walking, the anterior limbs do not usually play a part; they are held straight in front of the body and are employed only occasionally to aid in changing the direction of locomotion or to clamber over some obstruction. Out of the water Ranatra walks rather awkwardly. Its long slender second and third pairs of legs are articulated close together near the center of the body and the insect is frequently tilted over so that one extremity or the other strikes against the surface over which it walks. While Ranatra is capable of flight, it rarely if ever flies to lights at night as many other aquatic hemiptera do; I have never seen any specimen around electric lights where other insects are found in abundance.

Ranatras pass the winter in the adult state. I have collected numerous specimens in a small stream north of Ann Arbor late in November, but on visiting the same locality during a thaw in January following, although a diligent search was made in their favorite habitat among aquatic plants and by digging in the mud in the sides and bottom of the stream, I did not obtain a single specimen, although Zaithas and water boatmen were found to be quite common. Possibly the Ranatras burrowed more deeply than I could dig with the apparatus employed, although the general form of the animal renders this supposition improbable. Egg laying occurs in the spring. The eggs are long and narrow and furnished at one end with a pair of filamentous processes which, according to KORSCHELT, have a respiratory function. In ovoposition the female inserts the eggs into the stems of aquatic plants, or even into wood, the filaments projecting from the exposed ends.

Ranatras make a feeble sound by rubbing the bases of the anterior legs against the lateral processes of the prothorax. When a Ranatra is picked up in the fingers one can feel a slight tremor when the animal stridulates, although the sound is so faint that it cannot be heard farther than a few inches from the ear. What use, if any, is made of this sound is uncertain.

The method of sound production has been described by TORRE BUENO. The statement of this writer that the stridulation of Ranatra was not previously described is not correct, for the subject was briefly treated of by LOCY[1] in 1884.

The instinct òf feigning death, which is remarkably well developed in Ranatra, will be described in a subsequent paper.

III. REACTIONS TO LIGHT.

General Features of the Phototactic Response. When Ranatras are kept in a glass dish of water near a window they are usually to be found facing the light, often swimming towards it and repeatedly colliding with the side of the dish and clawing against the invisible barrier which blocks their course. These movements may be kept up, with intervals of rest, all day. When an artificial light is used the Ranatras may be caused to swim in any desired direction by placing the light in the proper position. In experiments with this species I have usually employed an ordinary 16 candle-power incandescent lamp attached to a flexible cord of wire which permitted it to be readily moved about at will. The work was carried on in a darkened room so that the specimens experimented with were exposed to light only from this source.

When Ranatras are taken out of water and laid on a table they generally feign death, and, while in that condition, they at first give no reaction to light. One may move the light about near them or hold it almost against their eyes without eliciting the least sign of a response. This apparent insensibility, gradually wears away, and after some minutes the movements of the light are followed by scarcely perceptible motions of the head. By passing the light back and forth laterally over the body the head may be caused to rotate laterally each time the position of the light is changed. These are the first movements that can be made to appear, and they grow more decided the longer the experiment is continued. A little later the animal may be made to respond by vertical head movements

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[1] Anatomy and Physiology of the Family Nepidae, *Am. Nat.*, 1884, p. 364.

when the light is passed back and fourth over the long axis of the body. When the light is in front the head is bowed down and when it is passed behind the body the head is tilted upward. Both the lateral and vertical movements are such that they tend to place the upper surface of the head at right angles to the direction of the rays. The vertical movements, like the lateral ones, are at first slight, and increase in vigor the longer they are caused to continue. The animal performs these movements with machine-like regularity and precision and without showing the least activity in any other part of the body. If the light is moved around the body in a circle the head will follow it with a corresponding rotary motion. If the light is in front and to the right of the animal the head will be tilted over to the right and at the same time pointed downward in front; or if the light is to the left and behind the animal the head will be tilted over to the left and raised up in front. For each position of the light there is a corresponding attitude of the head. The orientation of the head is remarkably precise. By carefully watching the tip of the beak with a lens as the light is moved it may be observed that a change of only two or three degrees in the direction of the rays produces a corresponding change in the direction in which the head is pointed.

After some time the movements of the head are accompanied by movements of the breathing tube. When the light is in front of the body the tube is lowered; when it is carried behind the body the tube is raised. These movements are at first slight but they become more decided and more regular the longer they are continued. Lateral movements of the breathing tube in response to light do not occur.

The next movements to appear are those of the limbs. The animal, after a time, shows irregular twitchings of the leg muscles, and soon afterwards slowly and unsteadily raises itself upon its legs and stands as if undecided whether to walk away or subside again into a state of repose. If now the light is passed over the body from side to side the creature will perform swaying movements each time the position of the light is changed. If the light is on the right, the back of the insect is tilted

over towards it, the right legs are flexed and the left ones extended (See fig. 1). Pass the light over to the left side of
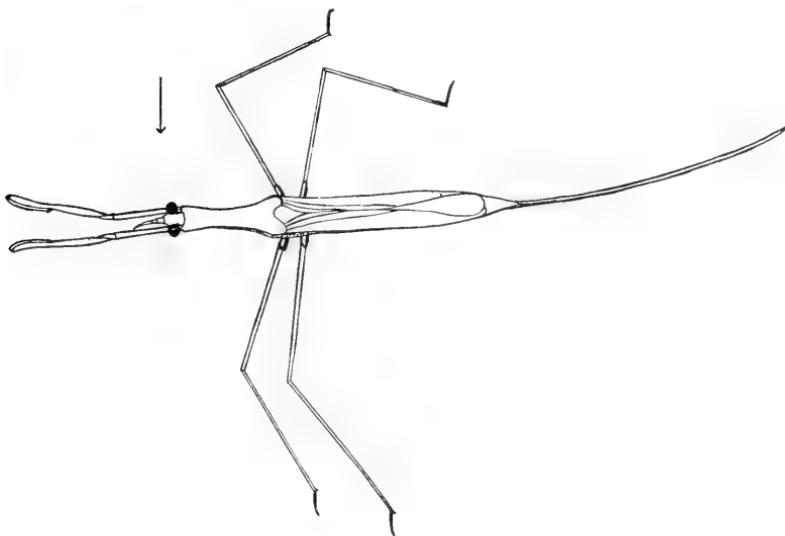
Fig. 1. Attitude of Ranatra when the right side is toward the light.

the body and the back tilts over to the left, the left legs become flexed and the right ones extended. For a short time after coming out of its feint Ranatra will usually sway back and forth as the light is moved over it without attempting to walk, but soon it begins to follow the light, at first with slow and unsteady steps, but later with more and more vigor, until finally its efforts to go towards the light become almost desperate, and it becomes oblivious to everything else.

Besides the lateral swaying movements which Ranatra performs when light is passed over the body from side to side there are equally pronounced longitudinal swaying movements when the light is passed back and forth along the axis of the body. When the light is placed behind the animal the body is raised up in front and the head held high in the air. Now place the light in front, and immediately the body is lowered, and the head bowed down, the grovelling attitude contrasting almost

comically with that assumed when the light is in the rear. By moving the light around the animal in a circle all combinations of lateral and longitudinal swaying movements may be produced, the body following the light by twisting about in a most curious fashion. With the light to the right and behind the animal the body is raised up in front, tilted over to the right, the legs on the right side flexed and those of the opposite side extended, the head turned to the right and the beak held high in the air. If the light is passed in front of the animal on the left side the head and body are both bowed down and tilted to the left, the left legs flexed and the right ones thrown in a state of extension. As with the head, so with the body, there is a certain attitude assumed for each particular position of the light.
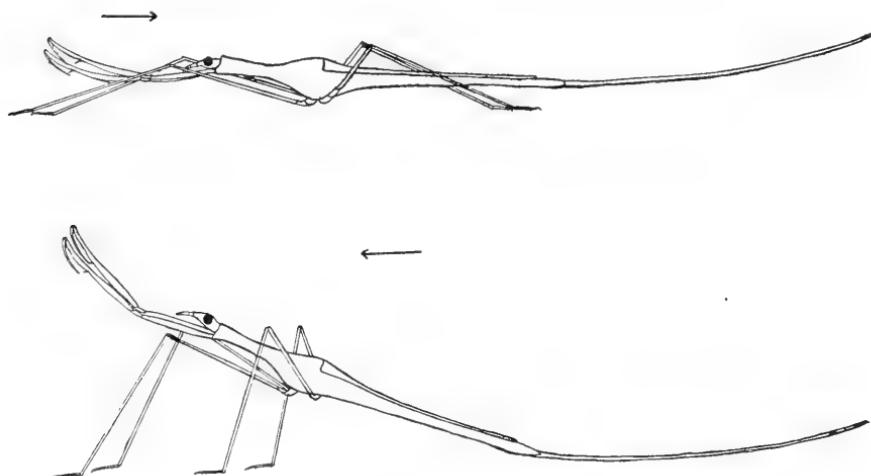
Fig. 2. The lower figure represents the position of Ranatra when the light is behind the body. The upper figure represents the position assumed when the light comes from in front.

Ranatras may be made to follow the light in any direction in the most slavish manner. By keeping the light to one side and a little behind the middle of the body the animal may be kept wheeling about in one spot, often, however, falling over on one side in its eagerness to get around. One reason for its awkwardness in this case is that as the light comes from the

rear the anterior part of the body is carried high in the air and the creature consequently easily loses its balance.

At any time after Ranatra has ceased to feign death it can be made to perform swaying movements in either direction, although these may be combined with efforts at locomotion. By carefully controlling the light, however, the tendency to loco-motion may be largely checked. By moving the light around the animal in a circle the tendency to turn back when the light is behind may be made to balance the tendency to go forwards when it is in front, and the animal simply sways around in its tracks.

Light seems to dominate entirely this creature's behavior when the phototactic reactions are once started. It does not manifest any fear or awareness of any object in its environment save the light which it so strenuously seeks. Its excitement increases the longer it is operated with, and after a time it may be picked up without feigning death, or with only a momentary feint. Not content with walking as rapidly as possible towards the light, the insect begins to fly towards it, always doubling up its fore legs in a curious manner before spreading its wings. The wings are never used, however, until the creature has sought for some time to reach the light by the ordinary meth-od of locomotion. Their employment marks the attainment of a high pitch of excitement in which the insect seems animated by an uncontrollable frenzy which lasts until it is checked by approaching exhaustion.

If a Ranatra is placed on its back it often has considerable difficulty in righting itself, and if near a light it will often walk towards it without turning over. Locomotion under these cir-cumstances is effected mainly by the anterior legs which are flexed dorsally at the middle joint. These legs are not employ-ed in ordinary locomotion, but when the creature is in an in-verted position they are used with considerable dexterity. By bending the legs dorsally the anterior end of the body is elevat-ed, and by the alternate movement of these appendages the insect walks along in a tolerably efficient manner. It will fol-low the light around in this way in any direction. When out

of orientation it reaches over to one side with the anterior leg nearest the light and pulls the body over until it is parallel with the rays.

2. *The Negative Reaction.* While under ordinary circumstances Ranatra is positively phototactic it may in certain conditions become strongly negative. If Ranatras which have been kept for several hours in the dark are brought back again into the light they usually show a marked negative reaction, but this negative phototaxis is never so violent as the positive sometimes becomes. Instead of appearing to be the result of reflexes which are comparatively direct and involuntary, the behavior of Ranatra gives the impression of being caused by the desire to escape from a situation which is unpleasant. It is perhaps remotely analogous to the action of a man when, after having been for some time in the dark, he instinctively turns away from the sudden glare of a strong light. The behavior of specimens after having been kept in the dark may be illustrated by the following experiments :

Twenty-five Ranatras which had been in a dark room for twelve hours were placed, one at a time, in a glass trough through which light was passed from an incandescent lamp situated a foot from one end. Each specimen was placed in the water in the center of the trough at rivht angles to the direction of the rays and let go in that position. If the specimen swam to the negative end, and within one minute returned to the other end when the light was changed it was classed as negative; and a similar criterion was employed for the positive reaction. If a specimen swam to one end of the trough and did not return to the other end within one minute after the light was changed it was classed as doubtfully positive or negative according to which end it first reached. Seventeen of the specimens proved to be negative; one was positive; four were doubtfully negative and two doubtfully positive. Out of the twenty-five specimens employed only one was unmistakably positive in its reaction, and this one swam to the positive end of the trough upon change of the light several times in succession. One spectmen did not swim to either end for five minutes. The Ranatras were then left exposed to the light of an incandescent lamp placed three inches from the end of the trough for one hour and forty minutes. At the end of this time all of the specimens were positive, The light was then held eight feet from the trough and the positive reaction still continued.

One of the specimens which showed a very marked negative phototaxis was singled out. During the time the others were being experimented with it was exposed to the light, and when again studied (after about a half hour's exposure) it showed a very evident negative phototaxis, but not so strong as before. After a time the negative reaction became so faint that it was scarcely distinguishable.

The specimen was then exposed to the strong light from a projection lantern. It showed at first a weak positive phototaxis which grew stronger the longer it was exposed, until it finally became almost violent. When exposed to the much weaker illumination from a 16 candle power lamp it still showed a marked positive phototaxis, but not so strong as when exposed to the light of a projection lantern.

At another time a Ranatra was placed in the trough which was exposed to the light of an incandescent lamp placed two feet from one end. The specimen immediately swam to the negative end of the trough. When the lamp was placed two feet from the other end the specimen quickly returned. The light was then changed repeatedly several times and each time the Ranatra would swim to the negative end of the trough, usually within four or five seconds. After a time its responses became slower and less definite. The light was then held close to the end of the trough and the responses became as prompt as before. It was changed from one end of the trough to the other forty-two times, and each time the insect within four or five seconds went to the negative end. Then it was left several minutes, after which its negative responses became less marked. When it was exposed to the strong light of a projection lantern it was still negative. It was then taken out of the water and laid on the table. In a few minutes it came out of its feint and showed the usual swaying movements when an incandescent lamp was moved near it, but it was very reluctant to walk. After 15 minutes of hesitation it became more active and showed an unmistakable positive reaction, and several times flew towards the light. When placed in the water again it still showed a strong positive phototaxis. The next morning (it was not in the meantime exposed to light, the room being darkened) it was markedly negative, and was driven from one end of the trough repeatedly by changing the position of the light. Then it was taken out of the water and placed on the table and an incandescent lamp was moved about near it to bring it out of its feint. It was a long time in awakening and for several minutes afterward it was disinclined to walk. When it did so it began to follow the light and soon became so excited that it would fly towards it repeatedly when four or five feet away. When put back into the water it was still positive and would follow the light in every direction. It was then exposed to the light from a projection lantern and became more strongly positive than ever, moving wildly towards the light even in the intense glare of the focus. Brought back to an incandescent lamp again it showed only a comparatively feeble response.

The negative reaction is associated with a condition of lowered phototonus. It is rarely shown except when the animal is in a condition of comparative sluggishness. When in great excitement, when its movements take place with quickness and vigor, Ranatra always shows a positive response. It never flies away from the light. Whenever it is wrought up sufficiently to use its wings, its reaction is invariably positive. The negative movements are slow and stealthy, often giving one the impression that the insect is attempting to sneak away unob-

served. The promptitude and decision of its negative move-
ments may increase up to a certain point if the insect is kept
close to the light, but when the movements begin to become
vigorous there is a transition to the positive type of reaction.
Often the advent of positive phototaxis is accompanied by a
marked accession of energy as if a strong dormant propensity
had suddenly been awakened.

The causes that produce the negative reaction are, as a
rule, those which lead to diminished activity and excitement.
Cold, exposure to darkness, the quieting effect of contact stimuli
lead to a condition of lessened excitability and, perhaps as a
result of this, to a negative reaction to light.

3. Head and Swaying Movements in Negative Phototaxis.
It would naturally be expected that the leg movements in nega-
tive specimens are the reverse of those in positive ones, and to
a certain extent this is true. It was thought not improbable
that the movements of the head would be reversed as well; but
it was found that in all cases in which Ranatras moved away
from the light the head reflexes take place exactly as in individ-
uals that are positive. Both in strong and in weak light, under
a variety of different conditions the head reflexes are the same
in kind regardless of the general sense of the response.

The swaying movements in negative phototaxis are readily
observed in Ranatras that have been resting quietly in the dark
for some time in a glass dish of water. If an incandescent light
be brought near them they are at first irresponsive. By moving
the light slowly about them the head reflexes are first induced.
Then there may be very slow and at first scarcely perceptible
movements of the legs, the second and third pairs being very
lazily extended on the side towards the light, and flexed on the
opposite side, the back being rolled over so that it more nearly
faces the light. On placing the light on the opposite side of
the body there is a very gradual extension of the legs previously
flexed and a flexion of those previously extended, the body
rolling over at the same time so that its dorsal surface lies more
nearly at right angles to the rays. The animal may be made
to repeat this performance many times in succession. After a

time its movements become more vigorous and it turns to walk away from the light; it can then be driven about in any direction at will.

The difference in the swaying movements of positive and negative specimens is mainly brought about by the different movements of the legs at the femoro-tibial joint. In negative specimens the legs on the side toward the light are extended at this joint while those on the opposite side are flexed; in positive specimens the reverse relation occurs. The rolling of the body is the same in both cases so that the muscles extending between the legs and the body are similarly affected in both kinds of reaction. The same relation probably obtains with the muscles between the joints of the upper parts of the leg. The vertical swaying movements of the body which involve the employment of these muscles are the same in both kinds of response. When light is behind a negative specimen the anterior part of the body is held high in the air as the insect walks away. When the light is held in front of the insect the anterior end of the body is lowered as it is turned from the light.

Only a part of the organism is subject to a change in the sense of its phototactic response. The head reflexes and swaying movements of the body are always such as to bring their upper surfaces more nearly at right angles to the direction of the rays, whether the organism as a whole is going towards or away from the stimulus. No matter how strong or how weak the light, or whatever may be the condition of the animal, these responses, if made at all, always occur in the same way.

4. The Effect of Contact on Phototaxis. As shown by the following records of experiments, Ranatra may be made negatively phototactic by means of contact stimuli. In one experiment seven specimens that were swimming against the side of the dish towards the window were picked up by their breathing tubes and dropped back into the water. At first they remained quiet but soon showed a negative reaction, swimming vigorously against the side of the dish away from the light. In about twenty minutes all but two had become positive again. They were all picked up by the breathing tube a second time

and dropped back into the water without touching any other part of the body. Soon all became negative without exception. After a few minutes they began to cross to the positive side of the dish one by one, and it was but a short time before every individual was positive. When I returned after an absence of an hour and a half all of the specimens were negative, although the light to which they were exposed had increased in intensity. Warm water was then added so as to bring the temperature of the medium up to 30° C. Four of the specimens soon became strongly positive. These were picked up by the breathing tube and dropped back into the water ; all became markedly negative. As specimens came over to the light side of the dish they were picked up and dropped as before, with the result, in almost every instance, of producing a marked temporary negative reaction. The next morning at 10 o'clock all of the specimens in this dish and in another that was beside it were swimming towards the light. They were all picked up and dropped back into the water when, without exception, they became negative. Soon they began to come over to the positive side of the dish and in about half an hour they were all positive again. They were all picked up and dropped a second time. All but two became negative. At 2:40 in the afternoon the specimens in each dish were aggregated into a dense bunch at the negative end. When stirred up some seemed positive and some negative, but their reactions were not decided. The temperature of the water in one dish was increased to 32° C. when about half of the specimens became positive in an unmistakable degree. When picked up and dropped into the water they quickly became negative. When they became positive again they were handled under the water without taking them out ; as soon as released they showed an unmistakable negative reaction.

I have tried handling positive specimens under water repeatedly. The effect is, in nearly all cases, to produce a change in the sense of the phototactic response.

The effect of contact and disturbance is very marked also on specimens while out of the water. This as well as other

features of interest is shown in the following experiments performed upon one individual :

The specimen was taken out of water from a darkened room where it had been placed the day before and placed near a light on a table. Soon it awoke and began to turn away from the light. The light was moved around it in different directions and, although the insect seemed at first dazed and walked about with no very decided tendency to go either towards or away from the light, it soon began to show a more pronounced negative reaction. It was then picked up by the breathing tube and placed at right angles to the rays from an incandescent lamp four feet away. During eight successive trials in which the right and left sides were presented alternately to the light to eliminate any tendency to turn to a particular side that might be due to habit, it turned in each case away from the light. Its movements were at first slow and stealthy. At the ninth trial it turned slightly towards the light, but reached the edge of the table before it had turned very far. At the tenth and several subsequent trials it turned towards the light and went up to it rather quickly. Its movements now became much more rapid. It was then placed ten feet from the light and still showed a positive response. It was then placed on the floor 22 feet away from the light, which was laid on the floor at the other end of the room. Although the light to which it was exposed was relatively very dim, the insect traveled to the light across the whole length of the room in nearly a straight line. When brought near the light the insect became more and more strongly phototactic and in about twenty minutes its efforts to reach the light became almost frantic. After a time it became apparently exhausted and settled down to rest.

It was then immersed in water and laid down on the table. Its movements were very sluggish and its responses to light slow. When placed at right angles to the rays it would slowly and stealthily creep away. It did this eight times in succession when the right and left sides were alternately placed towards the light. At the ninth and several subsequent trials it went towards the light. Then it was caused to follow the light about for a few minutes and soon it became quite excited. It was picked up and stroked but it could not be induced to feign death and as soon as released it made for the light, which was four feet away. It was then held in water for several seconds, but as soon as liberated it showed an unmistakable though not very strong positive reaction. It went up to the light, touched the bulb with its anterior legs, jerked back quickly as if burned, then stopped for a moment and walked away from the light. As the light was moved about, the insect would flee from it repeatedly as if it feared a repetition of its disagreeable experience. Soon, however, its responses became weak and indefinite ; its movements were sluggish. After a time it showed a positive reaction and began to follow the light all around the table. A little later it became much excited and flew towards the light repeatedly. The light was placed in a cylinder of water and the insect struggled to go towards it for ten minutes. It was then held in cool water for a short time and placed again on the table. After this experience it showed a marked negative response. The light was moved about the insect in various directions so as to keep it close to the body for about twenty minutes when positive phototaxis was again induced. When its reaction became very strong, the insect was picked up and stroked, but it feigned

death only momentarily and then resumed its efforts to go to the light.

A repetition of the experiment was followed by essentially the same result. When dipped in water again it showed a faint negative reaction. It would go towards the light when it was placed in front of the body or away from it when it was placed behind. Its general behavior was sluggish and it would perform only scarcely perceptible swaying movements when the light was moved over its body. Soon its negative reaction became more pronounced and it would turn away from the light every time it was placed to one side of the body. The insect was then placed under a bell jar near the light and upon my return after a two hours absence it was markedly positive. When dipped in water it showed a suggestion of a negative reaction, and for some time was apparently indifferent to the light. Repeated dippings failed to make the specimen more negative, and after a time a sluggish positive response began to appear. The light was then moved around it and finally the creature became very violent in the eagerness of its response and flew towards the light several times. When it was dipped in water it became sluggish. When placed at right angles to the rays it turned away from the light and started to do so a second time, but turned towards the light and went up to it. The same experiment was repeated three times in succession, and each time the insect turned at first away from the light and then towards it before having proceeded more than a few inches. After thirty minutes of positive reactions it was dipped in the water again. It went slowly towards the light but passed by it, and in several subsequent trials went away from the light; soon, however, it became weakly positive and in a short time its positive response was strong. After three hours of exposure to strong light it was still positive. When dipped into the water it showed at first a faint negative response but soon turned and went up to the light. Subsequent dippings failed to evoke a negative response.

It is not the effect of water in itself that changes the response, but the experience of being dipped in water. If the Ranatras are allowed to remain in the water they soon show a positive reaction. If then they are lifted out and put on the table they almost at once become negative if they are not thrown first into the death feint. Curiously enough, dipping into water is more effective in changing the sense of the response than handling or stroking the specimens in the air. Specimens which have been handled so much that they no longer respond to that treatment either by feigning death or by showing a negative response to light may usually be rendered negative after dipping into water.

As handling positively phototactic specimens usually causes their reaction to become negative, unless the experiment is repeated too often, it is probable that the change produced by dipping them in water is due to the influence of contact stimu-

li. It takes place independently of differences of temperature, and it cannot be satisfactorily accounted for by attributing it to chemical or osmotic changes produced by the surrounding media. Anything which makes towards the peculiar nervous condition which accompanies the death feint tends to produce the negative response. Dipping Ranatras into water usually throws them into condition of quiet when other influences fail, and the negative reaction is doubtless a result of the nervous state thus brought about. When a Ranatra is either placed in the water or removed from it, every portion of the surface of the insect is stimulated, and, although the stimulus upon no part is strong, the general effect may well be considerable. That the general integument is very sensitive is indicated by the fact that decapitated specimens often respond very strongly to the slightest breath of air.

5. *The Effect of Temperature on Phototaxis.* Raising the temperature tends to accentuate the positive phototaxis in Ranatra and lowering it tends to produce the negative reaction. In several experiments two dishes containing Ranatras were set before a window so as to receive the same amount of light. As the specimens had been previously kept in the dark, they showed a negative reaction. Into one dish warm water was poured raising the temperature from about 20° C to nearly 30° C. In a few minutes the specimens in the warmer dish became positive, the ones in the cool water still showing a negative phototaxis. Ranatras transferred to the cooler dish soon became negative while those which were picked up in the same way and dropped back into the warm water from which they were taken soon resumed their positive reaction. On the other hand, transferring negative specimens from cool to warm water produced in a short time a positive response. In cool water there is a marked tendency to form a dense cluster in the negative end of the dish. In warmer water the insects become more active and the groups are more apt to be broken up. Water at a temperature of 30° C usually stimulates them to very energetic movements. That negative phototaxis in Ranatra is induced by a reduction of temperature affords an illustration of

the general fact that circumstances which reduce the excitability of the insect tend to produce the negative reaction.

6. *Phototaxis Leading to Fatal Results.* Wishing to ascertain if Ranatra would continue to be positively phototactic if it were thereby led into a situation which exposes it to stimuli having injurious, if not fatal, effects I performed the following experiment.

A strong arc lamp was placed on a table so that the focus or space between the carbons was about five inches from the top, this elevation being chosen so that the specimen could not walk directly into the luminous arc although it was free to move about beneath it. As the lamp gave out a large amount of heat the insect in approaching the focus would he brought into a region sufficiently heated to produce a fatal effect if it remained there long. A Ranatra placed on the table, moved toward the light until it came under the focus, then starting off again, only quickly to return. It soon became wildly excited and made repeated dashes toward the light. Several times it flew towards it, but luckily escaped coming between the carbons. After a time it gave signs of being overcome with the heat, but whenever removed from the light it would quickly return. Its movements became weaker, although its efforts to go to the light were no less persistent. It became unable to raise its body off the top of the table as it walked, but used its legs to slide its body towards the light, and it would quickly re-orient itself when placed obliquely to the rays. Even its very last piteous efforts were devoted to pushing its body a little nearer the light. When no longer able to move it was placed in cool water, but it did not revive.

When a moth flies into a flame it is probably because it does not have time to check or change the course of its flight after it has drawn near enough to experience the injurious effects of the heat. The suicidal conduct of Ranatra, however, cannot be accounted for in this way. The movements of the insect are slow and deliberate enough, especially when it becomes weakened, so that it need not be carried by its momentum into a region from which it would otherwise flee. It reacts positively at every step, even when nearly overcome by the heat. Essentially the same phenomenon is seen in *Talorchestias* which when exposed to direct sunlight, keep jumping towards the light until the heat overcomes them and they die.

7. *Inhibition of Phototactic Responses by other Activities.* The phototactic responses of Ranatra which usually occur with such regularity and precision are sometimes checked when the insect is engaged in performing some other function. Specimens that have been following the light for some time often

stop to rub their eyes with their first pair of legs, using their claws in what seems to be an effort to scrape off some foreign object from the cornea. If a light is moved over an insect when it is engaged in this operation the swaying movements of the body will no longer be performed. The head reflexes are also sometimes inhibited, but usually the head can be kept moving about at the same time the insect is rather ineffectually attempting to rub its eyes The swaying movements are likewise inhibited when Ranatra stops to rub its wings or any other part of the body. These actions may be caused by daubing asphalt varnish upon the insect, when efforts are made to get rid of the offending substance. As soon as the cleaning movements are over the insect promptly reacts to light as before. It generally makes no attempt to do two things at once.

The phototactic response may also be inhibited by efforts to obtain food. Ranatras which are swimming towards the light can often be caused to discontiuue their phototactic efforts if several small insects are placed near them. If the phototactic activities are very lively and vigorous it is more difficult to divert the attention of the insect to the capture of prey. When attention is once directed to seizing the smaller insects the light is disregarded. When the prey has once been captured and the Ranatra is engaged in sucking out its juices little attention is paid to the light. The repast being finished the insect may resume its positive response.

Efforts to go towards the light are frequently inhibited by contact stimuli. When several individuals are put into a dish of water near a window they commonly cease, after a time, to swim towards the light and form a dense cluster in which they lie at all possible angles to the direction of the rays. If now the individuals are placed in separate dishes they soon show a positive phototaxis. When placed together again they quickly form a group as before. Contact stimuli not only inhibit positive phototaxis but they produce a negative reaction as we have already seen: the latter tendency however, is often held in check by the same cause by which it is brought about.

Phototactic activities may also be checked by the sudden

appearance of a large object in the field of vision. Ranatras that are swimming towards the light generally check their movements and lie perfectly quiet for some minutes as soon as they perceive one's approach, but if no movement is made near them they soon resume their phototactic activities. This inhibition of movement recalls that which in higher forms is often brought about by fear, but of the usual manifestation of fear in the efforts to escape from enemies by flight Ranatra evinces no sign.

Control in Ranatra probably amounts to nothing more than supplanting one instinctive tendency by another. The reactions of the insect to light seem to take place inevitably unless some circumstance calls into play some other equally stereotyped form of instinctive response.

8. The Effect of Hemisecting the Brain. Cutting the brain of Ranatra through the middle was accomplished by means of a fine needle ground down to a sharp edge. Only a small opening need be made, and there does not follow the profuse bleeding which results from making larger incisions. After hemisection of the brain specimens are easily kept alive for several days. Their behavior may be illustrated by the following records of experiments :

The brain was hemisected in three specimens at 8:45 A. M. In one minute or less they came out of their death feint; in five minutes they were picked up and stroked and then laid on the table. None feigned death for more than two or three seconds. At 9:25 they were still very restless and none of them paid the least attention to the light that was held near them. They all performed circus movements to a greater or less extent, due, doubtless, to the fact that the brain was not cut exactly through the middle. At 11 A. M., one flew out of the dish. They were all picked up and stroked again, but none feigned for more than a few seconds. When the light was moved about near them they would show no head reflexes or other decided response, although the light seemed to stimulate them in an indefinite way. During the next two or three days they continued the same restless movements and could be induced to feign death only for a few seconds. Definite responses to light failed to return.

The brain in three other specimens was hemisected at 12 M. They all soon came out of the death feint that was induced by handling them during the operation. At 1:20 P. M., when they were again observed, they were very restless. When picked up, stroked, and laid on the table they feigned death for one minute, four minutes, and ten minutes respectively. The next day they could not be induced to feign for more than a minute and they showed no definite response to light. They were also tried on each of the three following days and their be-

havior was essentially the same. Two specimens seemed to respond when the light was moved near them but when the rays were passed through water before reaching them no response could be evoked. It is probable, therefore, that their movements were the result of stimulation by heat. Ranatras with the brain cut through the middle, like those with the brain removed, are very sensitive to all sorts of stimuli, and they are set into action by causes which would produce no manifest effect in a normal individual.

Bethe[1] found that hemisecting the brain of *Carcinus* caused the phototaxis of the animal to disappear, although most of its other responses took place in a normal manner. I have found the same in several species of insects[2]. In the amphipod *Talorchestia longicornis*, which has a remarkably strong positive phototaxis, hemisection of the brain is followed by a complete loss of the power of orientation. Sensitiveness to light, however, is not entirely destroyed. If when a specimen is resting quietly in a shaded spot a beam of light filtered through an alum cell is thrown upon its eyes it usually responds by a few irregular movements. Since a large part of the fibers of the optic nerves cross in the brain, hemisection of this organ cuts off the main path of the impulses concerned in orientation to light.

9. The Effect of Covering the Anterior Half of the Eyes. Ranatras with the anterior surface of both eyes blackened over walk with the head strongly upturned and the anterior end of the body high in the air. Sometimes they stand nearly vertically, and several times I have seen them fall directly over backwards. Even when going towards the light the anterior part of the body is elevated, but not so much so as when the light is held above or behind the insect. When the light is moved backward and forward above the insect the body sways to and fro, and the head responds with the usual vertical reflexes. When the light is behind the insect the head and front part of the body are much elevated; if now the light is carried to the front the creature bows down only for a short distance instead of assuming the grovelling attitude of a normal individual in the same situation.

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[1] *Archiv f. mik. Anat.* 1897, **50**, 617.

[2] *Am. Jour. Physiol.* 1902, **5**, 211.

When Ranatra is compelled to walk on a glass plate while the light is held beneath the body it still carries the head and anterior part of the body high in the air.   The head and body are lowered somewhat if the light is placed below and in front of the insect, but not nearly so much so as in a normal specimen. If the light is passed to the rear beneath the glass plate the head and front part of the body are raised up.   Lateral head and body movements are performed in the usual way when the light is passed transversely over the posterior part of the body, but as the light is carried forwards these movements become less marked.   Similar results are obtained if the light is moved beneath an insect which is placed on a glass plate ; the responses become less evident and precise as the light is carried in front of the body.

Ranatras with the anterior surface of their eyes blackened over are still able to follow the light when it is in front of them, but their movements are hesitating and their orientation inaccurate.   This is a very natural result since the insects must be guided by the light which enters the posterior sides of the eyes.

10.   The Effect of Covering the Posterior Half of the Eyes. Blackening over the posterior surfaces of both eyes produces effects opposite to those observed when the anterior surfaces are blackened over.   The insect walks with the anterior part of the body lowered and the head inclined slightly downward.   If a light is held behind the insect the head and anterior part of the body are elevated, but not so much so as in a normal individual.   When the light is in front the body is lowered anteriorly and the head bowed down.   The same effects are produced when the Ranatra is placed on a glass plate and the light moved beneath the body.   The light is followed very readily when it is kept in front of the body ; if, however, the light is moved to the rear the insect experiences considerable difficulty in orienting itself and frequently travels for some distance directly away from the light before finally turning around.   Lateral movements of the head and body are readily brought about when the light is moved from side to side in front of the insect, but they become less pronounced when it is carried further back.

11. *The Effect of Destroying or Covering One Eye.* If one eye of Ranatra is blackened over or destroyed the insect in most cases no longer walks in a straight line but performs more or less decided circus movements towards the normal side. Under the stimulus of light the insect assumes a peculiar atti- tude ; the body leans over towards the normal side and the head is tilted over in the same direction. When a light is held oppo- site the normal eye the insect leans over towards it, and holds the legs nearest the light in a flexed condition while those on the other side of the body are extended. When the light is passed over the body transversely swaying movements are per- formed as long as the light is opposite the normal eye, but when it is passed to the other side of the body the insect sways back only to the middle position or slightly farther. The lon- gitudinal swaying movements of the body and vertical move- ments of the head are performed when light is moved forward and backward above the insect. These movements become less decided, however, as the light is held over towards the blind side.
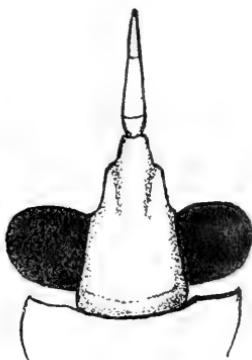
Fig. 3. Head of *Ranatra fusca* showing the almost stalked condition of the eyes.

If a light is held directly in front of a Ranatra with one eye blackened over the insect frequently does not travel straight towards it, but veers over towards the normal side until it comes to go in a quite different direction from that in which it

started out. In one experiment a Ranatra with the the right eye blackened over was placed at a distance of four feet from a 16 candle power lamp. In all of the twelve trials that were made it started on a nearly straight course towards the light as it was originally pointed. In all cases it veered to the left and naturally diverged from the straight path more and more the farther it proceeded. When a little more than half the distance to the light had been covered it corrected its course and proceeded towards the light again in a more direct path. This took place by two methods and usually occurred when the normal eye was looking away from the light. In this situation the insect would frequently stand for some time as if undecided which way to turn. In four instances it turned towards the right and proceeded again in the direction of the light. In eight cases it continued turning to the left until it had gone completely around in a circle after which it went up to the light.

Specimens with one eye blackened over present, however, marked individual differences of behavior. In some cases the insect walks toward the light in a nearly straight line. Ranatras which were taken late in the fall or early in the winter in most cases went nearly straight to the light while those experimented with in the early fall usually performed circus movements. This difference may have been due to accidental individual differences in the specimens, or it may have been the result of differences in age, the older Ranatras being better able to correct their course than the younger ones. The tendency to turn away from the blind side is manifested to a greater or less extent in all cases, but in many specimens it does not go so far as to produce decided circus movements.

If the whole of one eye and all but the posterior surface of the other is blackened over the insect in many cases is still capable of following a nearly straight path towards the light. A tendency to perform circus movements is more or less manifest and many specimens will go around in a circle repeatedly, especially when the light is near them. When all but the posterior surface of one eye is blackened over the insect is able to guide itself to the light nearly as well as when one eye is entire-

ly exposed. It may even follow the light by turning towards the blind side as the following experiment shows :

The right eye and all but a small part of the posterior surface of the left was thickly blackened over.. When the specimen came out of its death feint it walked nearly straight to the light. The light was then moved over toward the right side of its path several times, and the course of the insect was changed so as to continue going towards it. The light was then held to the right and behind the body and the insect circled around to the right. By keeping the light in the proper position the insect could be caused to keep circling around to the right in the same spot. The head and body in these movements were tilted over slightly to the right, but not so strongly as they are inclined to the left when the light is held on that side. The insect would perform circus movements to the left more readily than in the opposite direction, but it would make sharp turns to the right whenever it was necessary to maintain a position of orientation. When the light was placed behind the body the insect would usually turn around to the left to reach it. If, however, it was placed behind the body and a little to the right the specimen would turn around towards the right side.

12. *Reactions of Specimens with only Small a Part of the Lateral Surface of One Eye Exposed.* The right eye of a specimen was completely blackened over and all but a small part of the lateral surface of the left.

The insect was at first sluggish. When the light was held on the left side the head and body were tilted over towards it, and the specimen turned slowly to the left. When the light was placed two feet ahead of the specimen it moved very slowly and with the greatest hesitation, turning this way and that as if seeking to get its bearings, but going, nevertheless, nearly straight to the light. Although a decided tendency to make circus movements to the left was manifest, deviations in that direction were corrected by a direct turn towards the right side. When the light was held on the right side of the body the insect seemed confused and undecided which way to turn. When the light was held to the front and to the right so that the rays struck the body at an angle of about 45° the insect would not turn towards the light but moved about aimlessly until the left eye was presented to the light when it would turn to the left and go up to it. By keeping the light nearly in front of the body the insect would follow it all around the table. The experiment was then tried of holding the light farther over towards the right. The insect could then be caused to keep turning slightly towards the right in order to follow it. When the light was held still further to the right the insect still followed it. After a while it would follow it when held in a position to which it would not turn at the beginning of the experiment. After having got into the way of turning to the right side it would turn in that direction much more abruptly than at first.

A second specimen was treated in the same way, but it showed at first a pronounced negative reaction. It would pay little attention to the light except when it was held opposite the left eye when the insect would move away from it sidewise, much like a crab, by extending the legs on the left side and flexing

those on the right. When the light was held on the blind side the insect showed no inclination to turn away from it. The movements of the insect were slow, but, after about twenty minutes, it suddenly began to turn vigorously to the light and became much more active, following the lamp around with eagerness and rapidity. In several trials in which it was placed three feet away from the lamp it went towards it in nearly a straight line, correcting its deviations from a straight course, whether to the right or the left, by the appropriate turn. It soon became quite excited and several times attempted to fly. It would follow the light when it was in front and to the right side by turning directly to the right. If, when the light was reached, it was changed to some other part of the table the insect would turn around and make for it in nearly a straight line. After moving about in this way for some time it settled down so as to rest its body against the top of the table. The light was then placed near the specimen, but it paid no attention to it until it was moved opposite the left eye, when it began to move slowly away from it by crawling sideways. The whole character of the insect's behavior now became suddenly changed. It became sluggish and stealthy in its actions instead of vigorous and excited. It would respond to the light by moving sidewise instead of straight ahead, and only when the light was placed in a certain position. After moving the light around the specimen its negative reaction became more decided and then suddenly changed to positive. It would follow the light around either to the right or to the left, but if the light were held too far to the right side it would not turn directly towards it. The specimen had several other fits of reacting negatively when its conduct was essentially as described above. It was caused to become positive each time by keeping the light near the left eye. Its negative reaction would in each case grow more vigorous and then suddenly give way to the positive response. The appearance of the positive response seemed to indicate the attainment of a certain degree of excitement.

The differences between the negative and positive responses of the specimens experimented with are very striking. The peculiarites of the negative reaction are probably due to the fact that only when the light shines directly into the left eye is the stimulus strong enough to produce action. When out of the direct glare of the light the insect is content, and it gets away by the most direct method. In the positive reaction the insect is attempting to get more of the stimulus; it is in a state of increased phototonus, and each movement that brings it nearer the light tends to increase its activity.

13. Phototaxis as Modified by Experience and Habit. That Ranatra is able to modify its reaction to light as the result of experience was shown by several experiments. The attempt was made to determine if Ranatras which perform circus movements when one eye is blackened over would in time come to

travel to the light in a more direct course. A Ranatra with its right eye blackened over was placed on the top of a table three feet away from an incandescent lamp. Each time the specimen reached the lamp it was picked up by its breathing tube and placed in its original position facing the light. The course over which it traveled was in each case followed by a pencil. The paths taken in successive trials are represented in the accompanying diagram (Fig. 4).
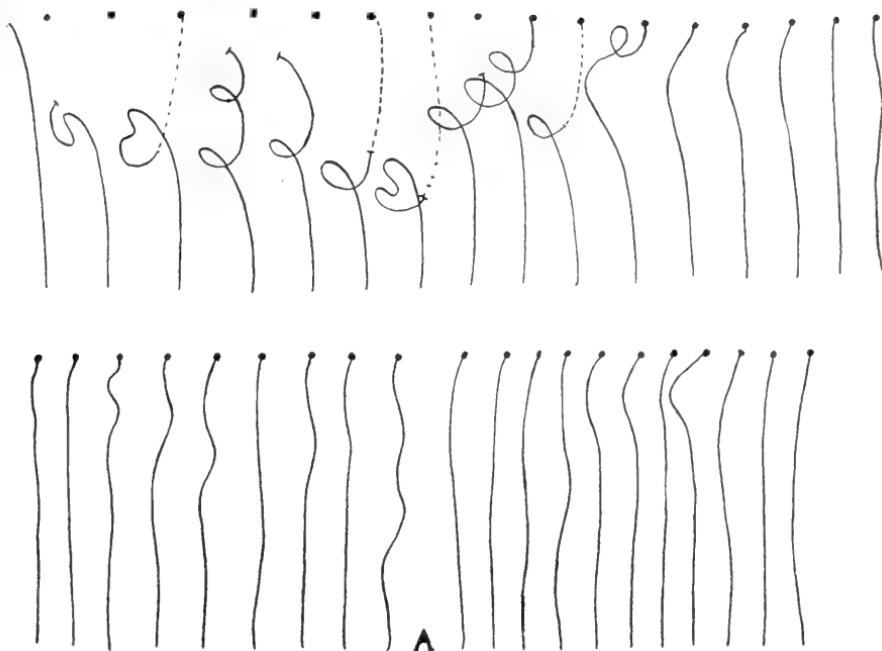
Fig. 4. Paths taken by a Ranatra in successive trips to the light. The position of the lamp is indicated by a dot at the upper side of each path. The cross lines indicate places where the insect took wing. When it flew directly to the light its course is represented by a dotted line. At *A* the experiment was discontinued for fifty minutes, after which the remaining tracings were taken.

The specimen showed a strong tendency to fly as it drew near the light, and after the tenth trial its wing covers were stuck down by asphalt varnish. After a few ineffectual attempts to raise the wings the insect gave up trying to use them and walked to the light more quickly and with fewer pauses. The

points on the path where the specimen took flight are indicated by a short cross line, and the position of the lamp is represented by a dot.

In the first trial the insect veered over constantly to the left, passed by the lamp and went off from the table before it turned around. In the following trials a marked tendency to turn to the left is also shown; frequently the insect makes one or more complete circus movements to the left before reaching the light. At the eleventh trial its course is corrected for the first time by a turn to the right side, but, instead of going straight up to the light, it performed a complete circus movement to the left before reaching it. The next time the course was corrected by a sharp turn to the right and the circus movement was dispensed with. At the next trial the course was corrected in the same way, and at the fourteenth attempt the insect deviated only slightly to the left side and then turned to the right to reach the lamp. In the following ten trials it reached the light by a nearly straight path. Whenever it began to turn away from the light to the left it corrected its course by a direct turn in the opposite direction instead of going around in a complete circle as at first. During the latter half of the experiment the insect became more excited and walked to the light more rapidly and with less hesitation and wavering. The experiment was discontinued at 12 : 10 P. M. and resumed at 1 P. M. The insect had not forgotten in the meantime how to reach the light by the most direct means. In eleven trials it went to the light in nearly a straight course, as is shown by the second series of tracings.

The specimen was then placed with its left side towards the light. In each of its successive trials it turned sharply to the left and went up to the lamp. It was then placed with its right or blind side towards the light. In the first two trials it turned sharply towards the light and went up to it. In the third trial it first turned towards the light, but soon veered over to the left and went away from the light instead of towards it. When placed again with its left side to the light it no longer went towards it as before. It manifested a decided negative phototaxis in fifteen successive trials. When placed facing the light, as in the first experiment, it turned sharply to the left and went away from it for three times in succession. Then a fit of positive phototaxis began to manifest itself again. In the fourth and fifth trials it reached the light by an irregular course. After this it went nearly straight to the light fourteen times. It was now allowed to rest for an hour and a half, when it was experimented with again. At the first trial it turned to the left, but corrected its course by a turn in the opposite direction and reached the lamp. In the second trial it went to the lamp in nearly a straight line. At the third attempt, after it had gone nearly to the light, in an almost straight line it turned away from it and went off in another direction. A fit of negative phototaxis now began to assert itself and in the next thirty trials it turned to the left and went away from the light. It was now nearly exhausted and could scarcely raise its body from the table. When near the light it would move in an excited manner in an effort to get away from it, but when it reached a darker region its movements became much slower, and it would soon come to rest. The experiments were then discontinued until the following day, when the specimen proved to be still strongly negative. After fifteen trials were made, in which it turned away from the light, except during a short fit of

positive phototaxis, when it turned twice towards it; the specimen was put back into the water. At one o'clock on the day following, it was taken out again. It still showed a decided negative reaction and turned to the left and went away from the light twenty-five times in succession. In nearly all cases after it had turned its back upon the light it went away from it in nearly a straight line.

After a rest of an hour and a half the asphalt varnish was removed from its eye. When placed on the table, three feet from the light, the specimen went towards the light and passed by it, but it turned around before proceeding very far and went up to it. After this it went to the light eleven times in nearly a straight line. The left eye was then blackened over. In the first two trials the insect veered slightly to the left, but reached the lamp by a turn to the right. In the third trial it turned sharply to the right and went off from the table. In the fourth trial it went straight to the lamp. After this another fit of negative phototaxis apparently seized it, for it turned from the light and walked away from it in numerous trials. It then became fatigued and the experiment was discontinued. It is worthy of note that while the insect, after one eye was first painted over, came to take a direct course to the light only after several trials, it went to the light, when the opposite eye was painted over in nearly a straight line at the first attempt. Unfortunately the fit of negative phototaxis which supervened prevented observation on this point from being carried out as fully as would be desirable. Owing probably to fatigue or frequent handling, the specimen became more prone to react negatively the longer it was worked with, until it no longer served the purpose of the experiment.

Other experiments showed a similar straightening of the course after a number of trials. As experiments on this subject were undertaken late in the season, most of the inviduals worked with went nearly straight to the light at the first trial. In one case a specimen went nearly straight to the light six times in succession; it was then taken up and its right eye given another coat of varnish to make sure that it was entirely covered. When put down again it seemed confused and performed a number of circus movements to the left. After several attempts, however, it came to travel to the light in nearly a straight line.

Similar experiments were tried on Notonecta with much the same results. These insects when placed on a table near a lamp travel towards the light with much eagerness. If one eye is blackened over they perform circus movements towards the normal side. After quite a number of trials, however, the Notonectas come to take a nearly straight course to the light. When they become deflected from their course they orient themselves by a direct turn in the appropriate direction. If the

lamp is kept over towards the blind side they may be made to perform circus movements in a direction opposite to that in which they would otherwise tend to go.
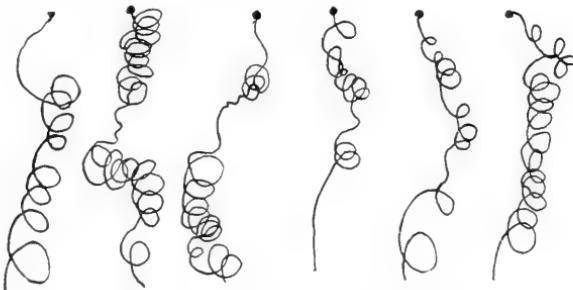
Fig. 5. Tracings of successive paths towards the light taken by a Notanecta, which had the left eye blackened over. After a number of other trials the specimen came to travel towards the light in nearly a straight line.

14. Formation of Habits of Turning. In working with Ranatras I have several times noticed what appeared to be a tendency to fall into habits of action, and I was naturally led to test the matter further by experiment. A Ranatra with its right eye blackened over was placed so that its head pointed directly away from a lamp three feet behind its body. As was to be expected, the Ranatra turned around to the left and went to the light. It was then picked up and placed in the same position ten successive times. In each trial it turned to the left and went up to the light as at first. In these and all subsequent trials the insect, when picked up, was turned alternately to the right and to the left before it was put down again. In this way the possibility that the results might be due to compensatory motions was eliminated.

Fig. 6.

After the first ten trials the insect was placed obliquely (at an angle of 45°) to the rays with its right side towards the light (position B in Fig. 6). In each of the ten trials that were made the insect turned towards the right or blind side, and went to the light. It was then placed
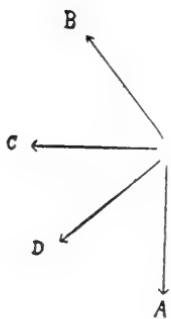
at right angles to the rays, the light falling on its right side as before (position C). In each of the ten trials made it turned towards the right as in the previous experiment. Then it was placed with its head pointing obliquely away from the light (position D), when it still turned to the right in each of ten successive trials. Finally, it was put back into its original position, A, with its head pointing directly away from the light. Instead of turning to the left, as it did at first, it turned to the right as in the experiment immediately preceding, and it repeated the performance in the same way ten times in succession. It was then placed in a slightly oblique position so that its left side was exposed to the light. Twice it turned to the right as before, but in the third and several subsequent trials it turned to the left. It would then continue to do so when placed back in its original position, or even with its right side slightly turned towards the light.

The experiments afford unmistakable evidence that when Ranatra has turned in any direction once it tends, *ipso facto*, to turn in the same direction a second time. The habit thus formed may even overcome the tendency to turn towards a particular side which is caused by blinding one eye.

IV. GENERAL CONSIDERATIONS ON THE PHOTOTACTIC RESPONSE.

The behavior of Ranatra in relation to light is, I believe, not without interest in relation to the general theory of the phototactic response. Many features of the phototaxis of this insect seem to afford strong support to the reflex theory. The perfectly definite and regular movements of the head in response to changes in the position of the light and the fact that these movements take place under all conditions in exactly the same way indicate that they are as machine-like as the most devoted partisan of the reflex theory of tropisms could wish. There is no evidence of choice, properly so called, in the performance of these actions. It is true that during the death feint they are no longer performed, but this affords no ground for regarding them as in any sense voluntary, since, as is well known, undoubted

reflexes are no longer performed in certain conditions of the nervous system.

The swaying movements of the body in response to changes in the position of the light seem almost as mechanical as the head reflexes. They are more easily inhibited, however, since they are often checked by efforts to rub the eyes, to clean the body, or to raise the wings after they have been fastened down, but they are immediately resumed as soon as the energies of the insect are no longer diverted to other actions. The swaying movements of the body are the result of a strong and definitely directed tendency to action which, when the insect is in a certain condition of tonus, it seems powerless to control. It is only when other instinctive responses are brought into play that the insect is able to overcome its phototactic activities.

The swaying movements of the insect vary, however, according as it reacts to light in a positive or a negative manner, but there is little evidence of choice as regards which mode of response is followed. In one nervous condition the insect is always negative; in another condition it is always positive. A Ranatra that is lethargic and sluggish reacts to light in a negative manner, while one that is highly wrought up and excited is always strongly positive. In intermediate states of excitement there is often a hesitation between the two modes of response, and the insect may exhibit alternate fits of positive and negative phototaxis of short duration. The power of one instinctive response to inhibit or overcome another may be considered as the first step towards the voluntary control. Choice as manifested by Ranatra is determined by which of two instinctive tendencies to action gains ascendency.

The mechanical nature of the phototactic response is further evinced by the effect of blackening over different parts of the eyes. When the posterior sides receive light the legs are extended and the anterior part of the head and body are held high in the air. When only the anterior sides receive light the head and body are bowed down. If light comes in only at the side of one eye the legs are flexed on the side towards the light and extended on the side away from it. It would almost seem as

if different areas of the compound eyes have special connection with particular sets of muscles such that when a given area is stimulated the muscles are set in action which bring about a particular attitude of the body.

We should bear in mind the possibility of interpreting the phototaxis of Ranatra as due to the fact that the light is sought because the insect derives from it an agreeable stimulus. We might regard the creature as so constituted that it derives pleasure from light and reacts toward it so as to get as much of this stimulus as psssible. Its behavior would then come under the head of what BALDWIN calls the "circular reaction." The movements of the head and body would be interpreted, according to this conception, as efforts to place the body in such a position that it can receive more of the desired stimulus. Whatever the position of the light Ranatra reacts towards it so as to place the upper side of the head more nearly at right angles to the direction of the rays. Both the head movements and the swaying movements of the body conspire to this end. And in this position it is probable that more light is received by the eyes than in any other.

Whatever may be the explanation of the process in physiological terms, it is evident that animals perform many actions simply because they derive pleasure from so doing. Such actions are, I am inclined to believe, not quite the same as simple reflex acts, even in such a creature as Ranatra. Simple reflex acts may, however, be accompanied either by pleasure or by pain, although neither of these states nor their nervous correlates determines the nature of the reaction. But in most cases of the pleasure-pain response the character of the nervous analogue of these states somehow determines whether movements producing them shall be continued or inhibited. Movements which bring agreeable stimulation are persisted in, while those which produce painful effects are checked. If any stimulus brings a pleasant sensation an animal is apt to make efforts to get more of that stimulus. If the creature possesses any power of association, movements bringing an increase of the stimulus are repeated and come to be performed with ever increasing

readiness. In view of the fact that insects are capable of forming quite complex associations and of guiding their action by their previous experiences there is no reason to balk at the admission of the possibility that an insect may seek the light because it thereby derives an agreeable feeling. Whether the phototaxis of Ranatra is to be interpreted as a form of pleasure seeking, or as a matter of direct reflexes, a sort of behavior forced upon the creature from without, is a question not to be decided without careful observation and experiment. That an organism travels towards the light in the direction of the rays, even though it goes from a brighter area into a darker one, is no decisive proof of the latter theory. We might interpret the orientation of an animal going towards the light as due, not to forced reflexes, but to a more or less voluntary effort to retain a maximum of stimulation. If a creature has reached that plane of psychic development at which it acquires a capacity of reacting with increasing readiness to stimuli which produce an agreeable effect, and of discontinuing those reactions which give rise to unpleasant results, it seems probable that it would not stupidly continue to orient its body and go towards the light if this were not associated with some sort of gratification. If the organism be capable of profiting by experience, we should expect such meaningless behavior sooner or later to be stamped out.

The impulses which are concerned in the reactions of Ranatra to light pass through the principal centers of the nervous system. The responses of the creature to light, if we consider them as reflex acts, cannot, therefore, be reflexes of a very simple kind. The impulses involved must pass from the eye to the brain, thence through the sub-oesophageal ganglion and the ganglia of the ventral nerve cord to the nerves supplying the legs. There are several links in the chain of neurons between the reception and the discharge of the stimulus, and there is abundant opportunity afforded for modification of the reaction through impulses coming from associated parts of the nervous system. As a matter of fact, we have found that the light reactions of Ranatra are modified in this way, as well as conditioned by the general nervous state of the animal. And

whatever changes in the nervous system may be due to the formation of associations or the effect of habit afford a further element in determining the nature of the phototactic response.

Now, while the light reactions of Ranatra take place to a large degree in a stereotyped and mechanical way, there is much to indicate that the insect seeks stimulation by light much as a bit of food or other object of interest is sought by a higher animal. A dog seeing a piece of meat on the other side of a fence makes a variety of efforts to get the prize. He runs up and down looking for a hole where he can get through or perhaps a low place where he can jump over. We cannot class his actions as direct reflexes in response to outer stimuli. His conduct is determined by the effort to secure a gratifying experience and various methods are employed to gain that end. A Ranatra seeking the light is much less resourceful than a dog trying to get on the other side of a fence, but, to a certain extent, the behavior of both animals is determined by interest in the object sought. As we have seen, Ranatra is able to go towards the light despite obstacles of various kinds. Even when one eye is totally blackened over and all but a small part of the posterior surface of the other is covered, many Ranatras are able to go towards the light in nearly a straight line. How is this done? A Ranatra in this condition is in much the same situation a man would be if one eye were blindfolded and he were attempting to reach a light by walking backwards. A man would accomplish this, if he had not previously seen where the light was situated, in a very indirect manner. By moving his head from side to side he could determine the darkest part of his visual field, and by facing in that direction he would finally be brought by walking backwards to the light. The darkest part of the visual field in this case is a rather indefinite thing as anyone may readily assure himself by trying the ex-experiment. A man's course towards the light would probably be very indirect, and it is not a little remarkable that so benighted a creature as Ranatra can reach the goal by so direct a course.

The two sides of the compound eyes must function differ-

ently in one respect, since in going towards the light the anterior side is turned so as to face the brightest part of the field of vision while the posterior surface of the eye is kept facing the darkest part. The impulses from the two sides of the eyes do not antagonize each other. The experiments of blackening over the anterior sides of the eyes show that the sides looking away from the light, as well as those looking towards it, play a part in orientation, although they must respond, so far as seeking intensity of stimulus is concerned, in opposite ways.

The method of trial and error plays, I think, only a subordinate rôle in the phototaxis of Ranatra, although in some situations it undoubtedly comes into play. There is a certain amount of random movement in the behavior of this form, but deviations from the direct path to the light are usually corrected by an appropriate turn, and not by making a lot of trial movements and following up the successful ones. Ranatras often show periods of hesitation between two directions of turning. Specimens that perform circus movements when one eye is blackened over usually manifest a decided hesitancy when they have turned so that the normal eye looks approximately away from the light. They often stop in their course, turn this way and that, often many times, and occasionally settle down to rest, as if in despair over the situation. Sometimes they turn directly towards the blind side and go to the light ; at other times they reach the light only after performing a complete circus movement to the left. When past the critical point their movements usually take place with little hesitation.

Specimens with only the posterior half of one eye exposed often turn slightly this way and that during the first part of their course, as if attempting to get their bearing. If they deviate either to the one side or the other they frequently stop, as if they perceived something to be wrong, turn back and forth several times, and then proceed nearly straight towards the light. In nearly all specimens thus treated one can detect a tendency to veer over towards the normal side, but there are equally obvious efforts to check deviations that are made from the direct path. There is an uneasiness which appears much like impa-

tience when a Ranatra that shows a strong positive reaction has deviated considerably from a straight path towards the light. When the normal eye looks away from the light the specimen may sway from side to side, back off, then go ahead again, growing continually more excited until finally it takes to flight. If the wings are fastened down to prevent their being used, the insect frequently spends several minutes before getting out of its dilemma. Sooner or later a fortunate movement is made which brings the creature into a situation such that the tendency to turn to a particular side meets with little opposition. Out of many trials made in this state of perplexity a successful one is finally made and followed up. Individuals vary greatly in their conduct in such a situation. Many correct their course before getting far out of orientation ; others, when they get out of line, turn back again with comparative readiness.

We might explain the function of the posterior side of the eye in orientation on the supposition that a movement which brightens the visual field brings about a reflex that causes a turn in the opposite direction. In this way deviations from the position that kept the darkest part of the field of vision in focus would be checked and the insect would, therefore, travel towards the light. It is more difficult, however, to explain the orientation of an insect in which a small area of the lateral surface of one eye is the only part exposed. If the insect moved so that the eye would look toward the darkest part of the visual field it would place its body with the blind side towards the light. If, on the other hand, it moved so that the eye would receive the maximum amount of stimulus, the opposite side would be brought toward the light. It is obvious that the insect moves so that the eye receives neither the maximum nor the minimum amount of stimulus, but is kept exposed to light of an intermediate degree of intensity, The degree of intensity varies, moreover, in every step of its course, so that there is no justification for explaining the orientation of the insect through the effort to keep a certain intensity of light constantly before the eye. It is remarkable that Ranatras so treated frequently go towards the light in nearly a straight line. Moreover, if the light is moved

during their progress they change their direction of locomotion so as to continue going towards it. If the light is not carried too far to one side the insect may be made to follow it around in either direction. In the specimens employed care was taken that every other part of the eyes was thickly covered except a small portion of the surface of one side, so there is no doubt that the movements of the insect were directed only by light entering at this point. The side of the eye in this case doubtless functions as it does in a normal individual, but it is difficult to explain satisfactorily the orientation of the specimen either through direct reflexes, or by the method of trial and error. Were the insect so constituted as to respond to an increase of light entering the left eye by a turn to the left and to a decrease of light by a turn to the right, we can understand how, when once pointed towards the light, a straight course might be preserved. If the insect turned towards the right there would be an increase of light entering the left eye which we might suppose stimulates the insect to turn in the opposite direcrion. Deviations to the left would cause a diminution of light entering the left eye, which we might suppose acts as a stimulus to turn to the right side. The right eye may be supposed to act, *mutatis mutandis*, in a similar manner. The numerous cases of reaction to shadows (*Scattenempfindlichkeit*) which are found among several groups of animals show that diminution in the intensity of light may act as a stimulus as well as an increase in intensity. If it be the variations in the intensity of light which afford the stimuli for turning in the one or the other direction, we can attribute to all parts of the eye essentially the same function. If the posterior side of the left eye is all that is exposed and a Ranatra that is facing the light turns to the right side the exposed part of the eye receives an increased stimulus which we may suppose brings about a turn to the left. A turn to the left of the median position, up to a certain point, would probably (owing to the body intercepting a part of the rays) diminish the light entering the posterior side of the eye, thus causing a turn to the right, In this way the creature might be supposed to maintain a straight course towards the light. A

similar explanation might be applied to the orientation of a Ranatra with only the anterior half, or in fact any other part of the eye exposed. The difficulty with this explanation is that an insect that started with an oblique orientation to the direction of the rays would tend to continue in that position, since a departure from it towards either side would be followed by a compensatory movement. If, however, light produces a constant effect upon the muscular tonus of the body, irrespective of affording stimulation by variations in intensity arising from turning towards different sides, we can better explain the fact of orientation. Take the case of a Ranatra with only the lateral surface of one eye exposed. Light entering the eye tends to increase the action of the flexors on the same side, and that of the extensors on the opposite side of the body. Through this action alone the insect, so far as light directs its movements, would continue to go around in a circle indefinitely. But as a matter of fact, as its circus movements bring the eye away from the light, they become checked and are followed by a turn in the opposite direction. What is the stimulus to this turn? Obviously there is a diminution of light received by the eye as it turns away, and we may regard this diminution as a stimulus to a movement in the opposite direction. This stimulus may be conceived, then, to overcome the tendency to the performance of circus movements, and thereby bring about an approximate re-orientation of the creature to the direction of the rays. That there is a conflict of impulses as the insect turns away from the light towards the side with the functional eye is evinced by the hesitancy, the swaying this way and that which often occurs when the creature has reached a position such that the amount of light received by the eye is materially diminished. The effect of light upon the tonus of the muscles of which the behavior of Ranatra gives so much evidence, fails to account for the fact of compensation in the movements of the insect. The responses to variations in the intensity of light, on the other hand, do not adequately account for the preservation of efforts to attain a parallel orientation to the direction of the rays. Each of these factors may, however, supplement the other in such a way as to

coöperate in the maintenance of a direct course towards the light.

But even if we invoke the aid of both the factors mentioned, we are not able completely to bring the phototaxis of Ranatra under the category of direct, mechanical reflexes. Consider the behavior of the Ranatra with its right eye blackened over, placed at right angles to the rays with the normal eye looking away from the light. The effect of light upon the muscular tonus of the creature would tend to make it turn towards the left side. But either at first, or after a few trials, the insect turns directly to the right and goes to the light. This is done with greater readiness after several trials are made ; soon the insect turns immediately after being set free. In these experiments the specimens were turned about, first one way and then the other, before being set down on the table, but this made no difference in the directness with which they turned towards the light. In many cases the insects would struggle to turn towards the blind side to get to the light before they were liberated from my hand. So far as could be observed, there was no preliminary feeling about, no employment of the method of trial and error; the insect seemed to retain awareness of the position of the light, since it immediately made for it by the shortest route as soon as it was liberated. The non-mechanical character of the response is further evinced by the fact that habits of turning towards a certain side may be persisted in in situations in which turning would otherwise take place in the opposite direction. The fact that Ranatras and Notonectas which have one eye blackened over come, after several trials, to dispense with circus movements towards the normal side and correct deviations from their course by a direct turn in the right direction affords further evidence for the same conclusion. We have seen that Ranatras which at first will turn only a slight way towards the blinded side when the light is carried over in that direction will make sharper turns after they have become accustomed to following the light around towards that side. These features of the phototaxis of Ranatra indicate that seeking the light has an attractiveness or interest much like that which catching prey has

for a higher animal. The phototactic movements of the creature are not merely stereotyped reflexes which the insect is involuntarily forced to perform. To get to the light is an end which is arrived at if not by one method, then by another.

The phototaxis of Ranatra comes, to a considerable degree, I believe, under the pleasure-pain type of response. Why a creature should be so constituted as to derive satisfaction from so stupid a performance as wildly chasing after a strong light is a subject that need not concern us in our present quest. The behavior of Ranatra presents the essential features of the pleasure-pain reaction of higher forms, and we are justified, I believe, in classing it under this heading. The fact that Ranatra will continue to follow the light even when it is brought thereby into a situation that produces a fatal effect does not necessarily exclude its conduct from this category. While it is true that animals tend to continue reacting towards stimuli that produce a beneficial effect and away from stimuli that bring about deleterious results, the rule is by no means absolute. In a state of nature Ranatras probably are rarely, if ever, exposed to conditions that produce as strong positive phototaxis as they show under artificial conditions in the laboratory ; and there seems to be no benefit that possibly can be derived from their strong propensity to seek the light. This propensity, like that of human beings for certain stimulants and narcotics, has probably not been evolved by natural selection for any useful purpose, but is an incidental result of the way the creature is constituted. Whether there is any connection between pleasure-giving acts which tend to be repeated and acts which secure some benefit to the organism closer than that which would naturally be established through selection may well be doubted. Neither an animal's direct reflexes nor its attempts to seek some source of gratification infallibly lead to securing some benefit; and the fact that a certain kind of behavior is persisted in until it brings about fatal effect does not *ipso facto* enable us to decide under which of these categories it falls.

It is the apparent telecity in the efforts of Ranatra to reach the light which it is difficult to understand according to a purely

reflex theory of phototaxis. This is a feature of the creature's behavior which, I am inclined to believe, we shall not be able to understand until we can explain the physiology of the process whereby certain stimuli when they have been received one or more times are sought either directly, or indirectly, by a more or less round-about method, while other stimuli when they are experienced one or more times come to be avoided. Did light afford a stimulus of an unpleasant nature, it is probable that the positive phototaxis of Ranatra would soon be inhibited. If the phototaxis of Rantra falls to a certain extent under the category of reflex action, as much in its behavior indicates, the reflexes concerned are in line with a strong instinctive interest of the animal in seeking the light. This interest may lead to successful attempts to get to the light in situations in which purely reflex responses alone would fail. It acts as a sort of regulatory agent in the conduct of the insect, bringing its actions to a successful issue, which could not be attained by a purely machine-like mode of response.

It is through instinctive interests in certain things rather than by simple or even complex reflex acts that the conduct of higher animals is mainly guided. The play activities of higher animals, for instance, are performed, not because they are reflex responses to particular things in the environment, but because the animal is so constituted that it derives satisfaction from their performance. An animal interest may be chained, by virtue of its organization, to certain ends, such as the capture of a certain kind of prey, or the construction of a particular kind of habitation ; but at the same time its conduct may show considerable plasticity as regards the methods by which these ends are attained. In instinctive behavior, as in the morphogenic processes which lead to the establishment and maintenance of the normal form of the body there is an apparent effort to reach a certain end result, despite obstacles and unusual conditions. The explanation of this peculiarity of animal behavior is a problem of fundamental interest. If we attempt to resolve highly complex modes of behavior into simple direct reflexes, we soon find ourselves at the end of our tether. Even in so apparently

mechanical procedure as the phototaxis of Ranatra we encounter peculiarities which indicate that we have not struck bottom in our analysis of the phenomenon.

In many ways the phototaxis of the Ranatra seems to be intermediate between purely reflex conduct on the one hand and conduct of the pleasure-pain type on the other. These two kinds of behavior seem to be harmoniously combined in many instincts, if not in most of the more highly involved modes of instinctive action. Just what the steps are which lead from the one to the other we do not know. We are still in want of a satisfactory explanation of the pleasure-pain type of response. When we are able to supply one we shall be in a position to give a more adequate interpretation of the phototaxis of higher forms than can be supplied at the present time.

LITERARY NOTICES.

Verhandlungen der Anatomischen Gesellschaft auf der Achtzehnten Versammlung in Jena. *Anat. Anz. Erganzungsheft zum 25 B.* 1904.

Schultze, O. Ueber die Entwickelung des peripheren Nervensysteme. 2-7.

The growing nerves in the embryo are syncytial in structure. The sheath nuclei are derived from the nuclei of this nervous syncytium. The plexus nervosus profundus of amphibian larvae (CZERMAK) is a sensory syncytium which is, and has arisen, *in continuo* with the developing nerve, and is not derived by a fusion of independent units. SCHULTZE's interpretation is in opposition to the neurone theory.

Koelliker, A. Ueber die Entwickelung der Nervenfasern. 7-12.

This paper is directly opposed to SCHULTZE's and in favor of the neurone theory. Each axone grows out as a process of a single nerve cell and the sheath nuclei are mesodermal in origin. This mode of development, the author asserts, is followed in Vertebrata, Arthropoda and Mollusca. The process may be simpler in lower forms.

In the discussion which follows these two papers, FRORIEP argues for the ectodermal origin of the sheath nuclei by a migration from the central system along the nerve roots. RETZIUS, BENDA, BALLOWITZ, HARRISON and DISSE cite various instances and observations in favor of the neurone theory. The necessity of experimental work upon the regeneration of the peripheral end of the severed nerve fiber is emphasized by ROUX and BARFURTH.

Joseph, H. Ueber eigentümliche Zellstrukturen im Zentralnervensystem von Amphioxus. 16-26.

The cells in question are the large cells in the anterior region of the nerve cord which v. KUPFFER called "dorsale Ganglienplatte." The author finds similar cells in the corresponding position in the caudal region of the cord. All of these dorsal cells, contrary to other authors who differ among themselves, are unipolar, and, in structure, correspond exactly with the "Sehzelle" of HESSE. They are not, however, capped with the pigment cell which is characteristic of the typical "Sehzelle." Their axones pass towards the periphery of the cord and probably enter the posterior roots. In the caudal region of the cord "Sehzelle" occur without the pigment cap, in which case they are identical in structure with the dorsal plate cells of the same region.

Hochstetter. Ueber die Nichtexistenz der sogenannten Bogenfurchen an den Gehirnen lebensfrisch konservierter menschlicher Embryonen. 27-34.

Schaper, A. Zur Frage der Existenzberechtigung der Bogenfurchen am Gehirne menschlicher Embryonen. 35-37.

Both of these papers on the embryonic fissures agree with the recent work of RETZIUS, MALL and GOLDSTEIN, who find no true fissures in the well preserved human brain during the period to which HIS assigned his "Bogenfurche."

Ramström. Ueber die Innervation des Peritonaeums der vorderen Bauchwand.

This study was made upon *intra vitam* methylene blue impregnations of the peritoneum and associated tissues. In the mouse, the peritoneum on one side the median line was mounted entire. No fibers from the phrenic were found entering this region. The innervation is wholly from the intercostal nerves, through a complicated system of plexuses.

Lubosch, W. Uber den Bau und die Entwickelung des Geruchsorganes von Petromyzon. 67-75.

This paper bears upon BLAUE's theory of the origin of the olfactory epithelium by a process of fusion of primitive cutaneous sense organs. The author conceives the olfactory buds of Petromyzon as representing a protracted ontogenetic process. The fundament of the olfactory organ is in the form of a bud-like differentiation of the integument. The organ develops by a repetition of this process. LUBOSCH considers that BLAUE's theory may be tenable upon the hypothesis that in the olfactory organ the nerve cell has maintained the primitive position, which it originally held in both olfactory and taste organs. Perfectly closed follicles are found in the nasal cavity of ten-centimeter larvae.

G. E. C.

Rutter, Cloudsley. Natural History of the Quinnat Salmon. *Bull. U. S. Fish Commission for* 1902, 65-142. 9 Pls., 13 Figs. 1904.

The objects of this investigation were to determine when young salmon should be liberated from the hatcheries, to discover a method for removing and fertilizing the eggs left in the fish after artificial spawning, and to fix the site for a new hatchery. Other matters of interest discussed are the activity of spermatozoa after the milt is mixed with water, the fertilization of the ova, care in handling embryos, alevins and their enemies, the fry and their food, parasites, and migrations, the food of young salmon and their period of growth. The adult salmon are treated in relation to migrations, changes after entering fresh water, sexual differentation, natural propogation, injuries and diseases, and death which ensues after once spawning. This contribution is of considerable scientific importance as well as being of practical value.

I. A. FIELD.

Kerr, J. Graham. On Some Points in the Early Development of Motor Trunks and Myotomes in Lepidosiren paradoxa (FITZ.). *Trans. Roy Soc. Edinburgh,* **41,** *Part 1 (No. 7), pp. 119–128, 6 plates, 1904.*

The author's observations support the conclusion that the motor spinal nerves of Lepidosiren first appear as strands of soft granular protoplasm, extending between the spinal cord and the myotome. These strands are not cellular. They later become fibrillated and invested by mesenchymatous sheaths. C. J. H.

Coggi, Alessandro. Le ampolle di Lorenzini nei Gymnofioni. *Monitore Zoologico Italiano,* **15,** *No. 249-56.*

On the basis of the figures and descriptions of the SARASINS, the author compares the "*Nebenohren*," or accessory lateral line organs on the head of Ichthyophis with the ampullae of LORENZINI of elasmobranchs, concluding that the organs are strictly homologous, thus strengthening the current belief in the archaic character of the Gymnophiona.

It will be recalled that the reviewer has suggested (this *Journal,* vol. **13,** p. 135) a similar homology between the ampullae of LORENZINI and a type of "small pit organs" found in the skin of the North American siluroid fishes, though the evidence for this relationship is not regarded as conclusive C. J. H.

Freidenfelt. T. Ueber den feineren Bau des Visceralganglions von Anodonta. *Lunds Universitets Arsskrift,* Bd, 40, Afd. 2. Nr. 5. Lund, 1905.

A detailed description of the neurones of the visceral ganglion and their connections, after methylene blue preparations, illustrated by four good plates. The author finds no true net-work (protoplasmic continuity of the older authors) in the neuropil, but refrains from expressing an opinion on the question of continuity of the neuro-fibrils of APÁTHY and BETHE. C. J. H.

Tumors of the Cerebellum.

Under the above title, the A. R. Elliott publishing Co., of New York, has re-printed six papers by Drs. MILLS, FRAZIER, DE SCHWEINITZ, WEISENBURG and LODHOLZ. While the clinical and surgical details do not fall within our limits, we call attention to the cases reported and to the summaries of literature as important contributions to the theory of cerebellar functions. C. J. H.

Banchi, Arturo. Di un cervello senze commessure e con funzioni apparentemente normali. *Archivio di Fisiologia.* Vol. I, pp. 614-618, 1904.

A brief statement of a remarkable case of cerebral malformation where the mental life seemed perfectly normal. An extended account of the case will shortly appear in the Archivio Italiano di Anatomia e di Embriologia J. C. B

Gross, Hans. Kriminal-Psychologie. *Leipzig*, *Vogel*, 1905. xii + 701. Zweite Auflage.

Although intended primarily for those who have professional interest in juristic problems and in the scientific side of criminology, this book of Gross' contains much that is of value to the comparative psychologist. In reading it one is likely to be impressed with the obvious need of psychological knowledge in the treatment of criminals and defectives. But, at the same time there is opened up, in thoroughly scientific systematic fashion, a vast realm of abnormal psychology which has been almost entirely neglected by scientific investigators, namely, the psychology of crime. The work is authoritative, and in this second edition it has been considerably improved in form and increased in value. R. M. Y.

Streeter, George L. The Development of the Cranial and Spinal Nerves in the Occipital Region of the Human Embryo. *Am. Jour. Anat.*, **4,** 83-116. 1904.

A study of numerous human embryos from the collections of HERTWIG, MALL, HIS and GOLGI. The period, 20-81 days, involves all the changes in form and relation from the time when the peripheral nerves are first capable of reconstruction to the time when the adult condition is practically established. The ganglionic crest in the cerebral region is from the first distinct from the trunk ganglia, though it is connected with the latter by a thin sheet of loosely arranged cells. The ganglia petrosum and nodosum are apparently adherent to thickened patches of the epidermis. The ganglionic crest of the tenth and eleventh nerves at first shows no signs of segmental arrangement. The latter nerves are found to belong to the same complex and alike have root ganglia and motor and sensory roots. In the course of development the sensory element comes to predominate in the cephalic portion of the complex and the motor in the caudal portion. The hypoglossal is like the ventral cervical roots in position and segmental arrangement. The ventral spinal nerves are developed earlier than the dorsal roots. G. E C.

Carlson, A. J. Contributions to the Physiology of the Ventral Nerve Cord of Myriopoda (Centipedes and Millipedes). *Jour. Ex. Zool.* **1.** 269-288. 1904.

In the ventral nerve cord of *Scolopendra* the conduction rate is greater in the antero-posterior direction. This antero-posterior differentiation, is most marked in the short types. Experimental studies on the localization of centres of control of important reflex functions.

G. E. C.

Mettler, L. Harrison. A Treatise on Diseases of the Nervous System, 989 pages, *Cleveland Press, Chicago,* 1905.

" The Neurone Doctrine is now an accepted fact."

After an introduction of 88 pages devoted to classification, etiology, symptomatology, etc., the writer describes first the neuronic diseases, beginning with the neuroses, hysteria, vertigo, neurasthenia, epilepsy, and all the other neuroses, the sympathetic included, and the system diseases—locomotor ataxia, the systemic motor palsies (including myasthenia), and the mixed afferent and efferent types.

The non-neuronic diseases (p 457–957) include the changes starting from the glia, vessels and sheaths, practically all the diseases of the peripheral nerves and diffuse and focal diseases of the nervous system. Alcoholism and some other toxic and infectious disorders with prominent participation of the nervous system come last (p. 959–971).

Notwithstanding this somewhat peculiar arrangement, METTLER gives a very readable presentation of the chief facts, general and clinical, in most respects superior to several of the books which are in the hands of many students In view of the excellency of the matter it is rather a pity that an essentially doctrinal issue should be at the top of every page—the distinction of neuronic and non-neuronic diseases, in the somewhat arbitrary sense in which METTLER makes his subdivision.

The illustrations are well chosen and very instructive. The book deserves recommendation. Lapses are relatively rare, as on p. 486, under BURDACH's column : " astereognosis, loss of reflexes and every physiological act that involves sensation, directly or reflexly, are diminished or abolished," when it is diseased.   A. M.

Child, C. M. Studies on Regulation. The Relation of the Central Nervous System and Regeneration in Leptoplana : Posterior Regeneration. *Jour. Ex. Zoology,* **1**, 493–512. 1904.

The presence of about half of the cerebral ganglion has both quantitative and qualitative influence on the reaction of pieces, and the efficiency of the brain in this respect is not localized. This efficiency is affected by the amount of nervous tissue present in the piece and not by the presence of a particular part of the nervous system. The influence of the nervous system upon posterior regeneration is quantitative only, and is not " formative " but indirect through the influence of functional conditions. In regeneration, also, the influence of the nervous system depends upon the amount present and not upon the presence of a particular part : a condition which argues against the idea of functional centers.   G. E. C.

A STUDY OF THE FUNCTIONS OF DIFFERENT
PARTS OF THE FROG'S BRAIN.

By WILHELM LOESER, M.D.

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As a contribution to the study of the comparative physiology of the brain, it seemed important to undertake a more detailed investigation of the functions of the different parts of the frog's brain than had hitherto been made.

The work done by me under the supervision of Dr. IDA H. HYDE—to whom I am under great obligations—can, at best, constitute only a small link, in the long and complex chain of comparative physiology. The experiments extended over a period of two and a half months, and the material operated on consisted of more than fifty frogs of the species *Rana temporaria*.

I employed GOLTZ's method, i, e., that of excising various parts, or aggregations of parts, of the central nervous system, and observed the resulting phenomena, particularly the deficiency phenomena. Both uni- and bilaterial excisions were resorted to. The animals were anæsthetized with ether until they would not readily turn over on the ventrum when put on the dorsum, but would respond only with convulsive jerks of the muscles of the limbs. For operations on the medulla the anæsthesia was carried further to prevent movements during the operation After the frog had reached this stage of anæsthesia, it was tied with its ventrum upon the frog board. A sponge moistened with ether and placed in front of the nares was sufficient to keep the animal in the desired stage of anæsthesia

during the operation. The skin over the cranium of the frog was first washed with a weak solution of bichloride of mercury, which was immediately removed with sterilized cotton and then with 95 % alcohol. The instruments and the hands of the oper- had been previously sterilized with 5 % carbolic acid, followed by 95 % alcohol.

An incision was made through the skin of the cranium, fol- lowing the mid-dorsal line. The skin was held apart by a pair of weighted hooks, and an opening was made with a small tre- phine through the cranium over the part of the brain to be re- moved. Since the two occipital arteries take their course later- ally, this opening was made as near as possible on the mid-dor- sal line of the cranium. With a delicate pair of forceps small pieces of the cranial bones were carefully broken away to make the primary opening of sufficient size for the operation. Great care was taken not to injure the meninges and the vessels of the choroid plexus therein. A 1 % solution of adrenelin was used with great success whenever injury to the choroid plexus, or even the internal carotid and branches caused profuse hem- orrhage.

A small pointed knife and a very fine needle were used for excising or burning the different parts. RINGER's solution was used to moisten the wound after the operation. No antiseptics were used in the wound, which was closed with sterilized silk sutures. The animals were kept isolated in moist moss, which was frequently changed. At first they were observed two or three times a day, but, after several days, once a day, and after seven to ten days, once every two days was sufficient. Most of the frogs were fed after the operation; a few—depending upon the nature of the operation—were soon able to catch flies. The observations were tabulated, dated, and later the post mortem findings were added. Two animals were used for each opera- tion, and the reactions compared with one another and with the reactions of normal frogs.

I seldom noted the immediate effects within one-half hour after the operation, since they were obscured by the effects of the ether. In some instances where it was quite evident that

the effects of the operation were present before one-half hour after the operation, I called attention to this fact.

Although I used a lens during the operation and post-mortem, I made no microscopical preparations of the specimens; therefore that degree of exactness which is obtainable by means of microscopical preparations was not reached.

By the term deficiency phenomena—as I use it in this article—I mean those phenomena which are normally present; but which are permanently—that is, for two and a half months —absent after excision of a part of the central nervous system, or permanently exhibited in a degree different from that in the normal animal.

OPERATIONS AND RESULTS.

I. The first operation consisted in removing one cerebral hemisphere. As a result, the animal displayed muscular weakness on the crossed side during the first three days. Thus the frog, when jumping, turned slightly toward the unimpaired side. Four days after the operation this temporary deficiency had permanently disappeared.

II. In the second operation I removed both cerebral hemispheres, and noticed as a result bilateral muscular weakness lasting about three days and accompanied by subnormal skin reflexes. No deficiency phenomena were noticeable the fourth day after the operation.

III. The third operation consisted in burning out the thalamus opticus of one side. The results were fewer voluntary movements ; bilateral defective sense of touch, especially in the fore-limbs ; almost complete loss of sight on the crossed side ; and weakness in the crossed legs. The first, second and fourth difficiencies improved slightly during the first two weeks, but the sight defect remained un-improved.

IV. After burning both optic thalami with hot needles, sight was almost completely abolished on both sides, and the animal was even more defective in the sense of touch and voluntary movements than after operation III. All three deficiencies showed practically no change during the two and a half months after the operation. The marked parallelism between the loss of touch-sensibility and voluntary movements was even more noticeable than after operation III. Flies put into the cage after operations III and IV were never caught.

V. The fifth operation consisted in unilateral burning out of the lobus and thalamus opticus. The result was a complete and permanent loss of sight on the crossed side ; forced movements straight ahead, which gradually improved ; transient retention of urine, and reduction in voluntary movements and touch-sensibility, exactly as noticed after removal of one thalamus opticus. Nearly all of the animal's movements were at first forced—straight ahead—during which it jumped higher and apparently with more vigor than normally. Stimulating the frog caused it to jump so powerfully that it frequently injured itself. It assumed,

moreover, abnormal positions of the limbs, for instance, adduction of both fore-legs until they almost touched each other.

VI.   The sixth operation consisted in burning both lobi and thalami optici. It caused total blindness on both sides; reduction in voluntary movements and touch-sensibility, as noticed after bilateral removal of the thalami optici and the other defects of unilateral excision of the thalamus and lobus opticus, but in a much more marked degree.   The abnormal retention of urine was one of the first phenomena to disappear; three weeks after the operation it was no longer noticeable.   The forced movements also improved, and were not noticeable after two weeks unless the animal was greatly excited.   The sight was permanently abolished on both sides.

VII.   The seventh operation—consisting in unilateral burning of the lobus opticus—caused slight defect in sight on the crossed side, straight forced move-ments, and abnormal retention of urine.   The last two phenomna were as indi-cated in operation V.   Sight was normal on both sides after two weeks.

VIII.   After the next operation in which both lobi optici were removed, the trifling defect in sight was bilateral, the straight forced movements were stronger, and the retention of urine more pronounced than after unilateral excision of the lobus opticus.   The forced movements and the abnormal retention of urine improved as indicated in operation VI, and the slight bilateral defect in sight improved within ten days so as not to be detected.

IX.   The ninth operation, which consisted in removing the anterior half of the two lobi optici, showed, during the first two weeks, the abnormal retention of urine and slight bilateral loss in sight, as noted under bilateral removal of the lobi optici.   Later, until two and a half months after the operation, sight was normal on both sides, and urinary retention gradually disappeared during three weeks after the operation.

X.   In the tenth operation the posterior half of both lobi optici was re-moved, and the result was that the forced movements became apparent as noted in operation VIII.   Later these were present only when the frog was extremely excited.

XI.   By removing both optic thalami and the anterior half of the lobi optici all the phenomena as noted under bilateral removal of the thalami and lobi op-tici, with the exception of the forced movements, were noticed.

XII.   By burning the dorsal half of both thalami and lobi optici sight was only slightly injured for two weeks, whereas the abnormal retention of urine, the forced movements, the depression of voluntary movements and touch-sensibility were injured according to the amount of nerve tissue removed.

XIII.   After bilateral removal of the cerebellum, the jumps became very unsteady and were weakened in force but not much reduced in rate.   Most of the time the frog lay stretched in contact with the floor of the vessel and cov-ered with moss.   The unsteady and weakened condition of the limbs persisted in a marked degree two and a half months after the operation (especially when the frog was greatly excited).   The frog's hibernating tendency persisted two and a half months after the operation and it did not succeed in catching flies put into its cage.

XIV.   Unilateral excision of the cerebellum caused a number of phenomena which also appeared more pronounced after unilateral excision of the medulla an-

terior to the origin of the vagus group; the limbs of the crossed side—especially the posterior one—were abnormally extended and abducted, locomotion was always towards the homonymous (operated) side. The spine was slightly bent, concave towards the homonymous side in the thoracic region. Though the forced position of the limbs of the crossed side and the curved state of the spine improved considerably in one week after the operation, yet they, together with the squatted position of the body, and locomotion, remained quite characteristic two and a half months after the operation.

XV. Bilateral excision of everything anterior to the medulla leaves the croak, the turning-over, the swallowing and heart-action reflexes, the sense of equilibrium and respiration intact. The croak and turning-over reflex could hardly be elicited during the first few days, but they were normal after one week. If the anterior portion of the medulla was also removed, apnoic pauses alternated with periods of normal respiration. During such a pause, the animal remained quite motionless for about five minutes. To avoid injury to the medulla, it is best to burn off the cerebellum after everything anterior to it has been removed.

XVI. After unilateral excision of the right side of the medulla anterior to the calamus scriptorius abdominal respiratory movements on the homonymous side stopped, whereas the narial and oral as well as swallowing movements were still normal.

The animal assumed a flat position and the head and homonymous side were lower than other parts of the body. The legs on the crossed side, especially the posterior one, were far extended and abducted; and the homonymous legs, especially the front one, were superflexed and adducted. Forced rotary movements around the sagittal axis of the body and towards the homonymous side were present as the sole movements on land and in water. The eye reflex to pressure on the homonymous side of the body was abolished, but was normally present on the crossed side. The crossed eye was turned up and outward, and the homonymous one, down and inward. The homonymous eye was turned up synchronously with inspiration, and down with expiration. The nictitating membrane of this eye was evidently beyond the control of the frog since it covered the eye, especially when it moved downward. The spine and neck were curved as after unilateral cerebellar excision and tremors were present in the limbs on both sides, but were more pronounced in the weaker legs of the homoymous side. A weakened croak reflex still persisted.

These defficiencies were almost entirely confined to the homonymous side. Sight was perfect on the crossed side, and although the eye reflex to pressure was abolished on the homonymous side, the animal still saw with this eye. The rotating table reactions were complex and will therefore be described in greater detail. One half to five hours after the operation the animal did not react on the rotating table with either head or body movements. Twenty-four hours later, when the table was rotated in a clock-wise direction, i. e., towards the operated side of the frog, the animal held its head in anti-clock-wise direction during rotation ; after rotation, the head was brought back beyond the sagittal axis of the body in a clock-wise direction. On rotating the table in anti-clock-wise direction, no head movement was produced during and after rotation, but a slight circular movement of the body in anti-clock-wise direction was seen after rotation. Forty-eight hours afterward, while rotating the table in a clock-wise direc-

tion, a slight movement of the head, as previously noted, was seen during and after rotation of the table ; and sometimes a circular movement of the body in clock-wise direction, after rotation of the table. While rotating the table in anti-clock-wise direction, no head movement was seen, but a slight circular movement of the body in anti-clock-wise direction appeared after rotating the table.

Abdominal respiration ceased during rotary movements, but subsequently it was resumed on the operated side. Fifteen days after the operation, by means of vivisection under very slight anaesthesia and exposure of both lungs, I observed that only the crossed lung respired. In the meantime, the characteristic position of body and head had but slightly improved, and was as pronounced as ever when the frog was excited. The rotary movements around the sagittal axis, which began about ten minutes after the operation, at the end of two days had diminished, but were aroused by the slightest stimulation, even by sight or movement, on the rotating table toward the crossed side ; they could also be inhibited in part or completely by touch and movement on the rotating table toward the homonymous side.

After three days the position of head and body was temporarily normal and the superflexed or superextended legs respectively were also temporarily brought back to their normal position. After five days the rotary movements showed themselves only when the frog was jumping ; the animal usually made a complete circuit around its sagittal axis during the jump. Three days later the frog sometimes landed on the dorsum after a jump ; and the croak reflex became stronger. By the tenth day the rotary movement was manifested by the fact that the animal landed on the side after a jump. The jumps never became as strong and skilled as before the operation. The position of the head, body and legs had improved ten days after the operation, although still quite abnormal. The position of the eyes and the movements of the homonymous eye and nictitating membrane had improved very little during the fifteen days following the operation. In fact, no appreciable improvement was noticeable after ten days. The defects were least noticed while the animal was at rest.

XVII. Unilateral excision of the right side of the medulla, anterior to the origin of the vagus group left the croak reflex and abdominal, narial, and oral respiration movements intact on both sides. It caused rotatory movements around the sagittal axis, the peculiar flat position of the front part of the body and head, the characteristic position of the limbs, the eye reflex, the position of the eyes, the movements of the homonymous eye and nictitating membrane and the rotating table reactions exactly as stated in operation XVI. The apnoic pauses in the abdominal respiration after rotary movements around the sagittal axis, were less pronounced.

XVIII. Unilateral excision of the right half of the medulla from a point posterior to the origin of the vagus group down to the calamus scriptorius, left the croak reflex intact. The abdominal respiration was slightly injured on the homonymous side and intact on the crossed, as was proved by vivisection and exposure of both lungs under very slight anaesthesia. The eyes were normal on both sides, excepting that the pupil of the homonymous eye was extremely contracted. The characteristic position of the body, head and legs was present in a lesser degree than after operation XVII. The rotatory movements around the sagittal axis were absent, but the animal landed on the homonymous side, after

jumping, in a position at right angles to the direction in which it started. The rotating table reactions were normal in both directions. The abdominal respiration remained weakened on the homonymous side during the fifteen days following the operation; after which the post-mortem was made. The position of the body, head and legs had gradually improved at the end of the first week so that they were almost normal. From that time until the fifteenth day no further changes were observed in these or in the unskilled and weak action of the homonymous limbs. The homonymous eye remained permanently constricted.

XIX. A unilateral excision of the middle third of the medulla, including the origin of the vagus group, abolished abdominal respiration on that side but left a weakened croak reflex. The pupil of the homonymous eye was contracted, otherwise the eyes appeared normal. The position of the head, legs and body, and also the locomotion agreed with those noted under operation XVIII. The rotating table reactions were normal and no rotary movements around the sagittal axis were exhibited. The croak reflex was quite normal two weeks after the operation.

XX. Bilateral excision of the middle third of the medulla, including the origin of the vagus groups abolished the croak reflex, turn-over reflex, and the abdominal respiration on both sides. The heart, though beating strongly ten minutes after the operation, became quite feeble two hours later and stopped at the eighth hour after the operation. The respiratory movements of the nares and mouth remained bilaterally present, increased very much in rate and force and exhibiting asphyxia symptoms toward the end. It was impossible to keep these animals alive longer than eight or twelve hours even when the water surrounding them was frequently changed. After this operation a complete inversion of the stomach and oesophagus, with prolapsus into and even outside of the mouth occurred. The pylorus was the most anterior portion of the prolapsus. I placed a dead fly on it and was interested in seeing it surrounded by slow peristaltic movements. The pancreas, stomach, duodenum, and the adjoining small intestine were also involved in the prolapsus. The stomach was distended to twice its normal size. The peculiar position of the head noticed after the different operations on the medulla was most conspicuous after this operation. The head pointed into the ground and formed an obtuse angle with the body. The urostyle was always less prominent after medulla injury.

XXI. Excision of everything anterior to the spinal cord abolished the respiratory movements, sense of equilibrium, eye, sight, croak, swallowing, heart, and the turning-over reflexes. A stimulus was immediately answered by co-ordinated movements. It was answered sooner and with greater certainty than when the higher portions of the brain were intact. The heart action gradually faded away during the five hours following the operation.

XXII. The excision of everything down to and including the anterior portion of the spinal cord almost to the origin of the brachial plexus caused all of the deficiency phenomena enumerated under operation XXI and in addition caused the co-ordinated movements to fade away. They failed as soon as the anterior limbs were incapable of supporting the body and helping the posterior limbs in their efforts.

Discussion and Conclusions.

The removal of one or both cerebral hemispheres proved that the motor centres of the cerebral cortex of the frog are of minor importance and the sensory centers scanty. The fact that a frog deprived of both cerebral hemispheres caught flies proves that the reflex connection of the optic nerve with the innervation of the snapping and swallowing apparatus is not located in the cerebrum. Although GOLTZ[1] observed a loss of muscular sense for several days in his dog deprived of both cerebral hemispheres, no such defect was visible in my frogs from which both cerebral hemispheres had been removed. The decrease in voluntary movement and sensitiveness to touch which existed for a few days, I attribute to disruption of association fibers and not to destruction of motor or sensory areas.

In connection with my results, I may mention that BICKEL,[2] using chemical agents, and both kinds of electrical stimulations, was unable to produce paralysis in the pigeon or frog unless the current was excessively strong. BICKEL further concludes that in turtles the cerebrum does not regulate movements but has a motion-inducing (bewegungsanregend) in fluence. ADAMKIEWICZ[3] also states that an animal deprived of the cerebral cortex carries on all bodily movements normally if it is artificially induced to perform them. BARY[4] determined that the new-born child lacks the principal group of motions which are controlled by the will. Moreover, SCHRADER[5] demonstrated that frogs deprived of the cerebrum behave, after several days, like normal frogs, and GOLTZ showed that his dog deprived of the cerebrum was essentially normal, excepting that the higher cerebral functions—memory, deliberation, intelligence, pleasure and envy—were absent.

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[1] GOLTZ, F. *Pflüger's Archiv*, **51**, 570, 1892.

[2] BICKEL, A. *Pflüger's Archiv*, **72**, 190, 1898, and *Archiv für Anatomie und Physiologie*, **52**, 1901.

[3] ADAMKIEWICZ, A. *Neurologisches Zentralblatt*, **22**, 12, 546.

[4] BARY, A. *Archiv für Anatomie und Physiologie*, 341, 1898.

[5] SCHRADER, M. *Pflüger's Archiv*, **41**, 75, 1887.

Opposed to my observations are those of STEINER[1] who states that the frog deprived of the cerebrum does not take nourishment spontaneously or carry on willed movements, and that the region presiding over these functions is in the posterior portion of the cerebrum.

The operations on the optic thalami indicate that these, more than any other portion of the frog's brain contain the primary nuclei of the nervus opticus, and that this nerve joins their ventral, rather than their dorsal portions. The permanent reduction of voluntary movements and tactile sensibility noted after excision of these bodies may be regarded as an important deficiency phenomenon, and I assume that the principal reflex ganglion of the sense of touch is located in these bodies. The reduction in voluntary movements must be attributed more to the presence of a motor nucleus in these bodies than to a destruction of associative connections which they have with other motor ganglia, for this phenomenon lasted during two and a half months.

My results and conclusions in regard to the optic thalami strengthen those obtained by SCHRADER[2] who states that frogs deprived of the optic thalami show a decrease in voluntary movements and sensitiveness to touch and complete blindness. My observations and conclusions do not agree with those of STEINER who admits that there seem to be primary elements of sight in the optic thalami of the lizard, but show instead that this is contrary to what is found in the frog; and they do not agree with the results of SELLIER and VERGER[3] who found that in the dog injury to the optic thalami causes transient disturbances of the muscular and touch sensibility.

The operations on the optic lobe showed that the anterio-ventral quarters of these bodies are in close association with the retinal part of the optic thalami, but that the chief center of the

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[1] STEINER. Die Functionen des Central Nervensystems und ihre Phylogenese, Abtheilung 4.

[2] SCHRADER, M. *Pflüger's Archiv*, **41**, 75, 1887.

[3] SELLIER and VERGER. *H. C. R. Societés de Biologie*, Mai, 522, 1898.

optic nerve is not in the optic lobes. The fact that the slight defect in sight disappeared two weeks after the operation, indicates that its cause was inhibitory stimuli. By excising the lobi and thalami optici unilaterally it was proved that the nervus opticus of the frog crosses completely at the chiasma. The abnormal retention of urine and the straight forced movements—always noted after excising the anterior and posterior half of the lobi optici respectively seemed to be caused by abnormal stimuli due to direct loss of association fibers. It indicates that the anterior part of the lobi optici is in close connection with the sacral urinary ganglia and the posterior, with some important motor nucleus.

My observations and conclusions regarding the optic nerve agree with those of SINGER and MÜNZER[1], WIEDERSHEIM[2] and SCHRADER, who found that in fishes, reptiles and amphibia the decussation of the second nerve seems to be complete, and that the centres of the nervi optici are located in the thalami optici. My results agree neither with those of DONALDSON[3], who states that the frog loses the power to avoid obstacles when the optic lobes are removed nor with those of LANDOIS[4] who says that destruction of the optic lobes in birds, amphibia and fish is followed by blindness.

The unsteady and weak jumps, flat position of the body and the tendency to abnormal hibernation, following bilaterial cerebellar excision, I believe to be due to the weakened condition of the limbs, to a loss of muscular tone, as well as to a loss of timely sequence or co-ordination and gradation according to the strength of the contractions, i. e., sensory ataxia. It seems that these deficiency phenomena are to be explained by the absence and modification of normal impulses proceeding from or going to the cerebellum. Anatomically, the explanation might

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[1] SINGER and MÜZNER. *Denkschriften der mathematik-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften,* **55,** 1888.

[2] WIEDERSHEIM. Vergleichende Anatomie der Wirbelthiere, 2nd Edition, 335, 1886.

[3] DONALDSON, H. H. American Textbook of Physiology, 708, 1897.

[4] LANDOIS, L. Textbook on Human Physiology, 805, 1904.

be offered that the neuron-complex, consisting of an afferent path to and an efferent path from the cerebellum and the ganglionic structures intervening, had lost important elements and that thus the function of the whole neuron-complex had been destroyed.   This represents absence of normal impulses and may explain the defects after cerebellar excision.   It is, however, impossible for the remaining neurons to make connections with other surrounding normal neurons and thus take up part of the functions formerly possessed by the destroyed neuron-complex.   There evidently was a slight trace of this modification of impulses present two months after cerebellar excision, since the position of the body and the condition of the limbs had improved two months after the operation.   The fact that the condition of the body and limbs became worse on stimulation, probably indicates that the modified paths were fairly able to master the situation during rest but were not capable of doing so during excitation.   It has been observed in many instances that stimulation brings out to their fullest extent the defects which are in part hidden by the vicarious activity of the modified paths during rest.

After unilateral cerebellar excision, the bilateral defects were confined to the homonymons side.   Uni- as well as bilateral excisions of the cerebellum have shown that it does not possess the function of maintaining the equilibrium or any intellectual functions.   The former function is located in the medulla, and the latter—the small amount that the frog possesses—probably in the scantily developed cerebrum and in the optic thalami.

My conclusions regarding the cerebellum do not agree with those of Steiner[1] who states that symmetrical removal of the brain down to the medulla in the frog produced no changes in the motor activity of the extremities.

Bilateral excision of everything anterior to the medulla shows that, although the croak and turning-over centers seem

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[1] Steiner, J.   Untersuchungen über die Physiologie des Froschgehirns. *Braunschweig,* 1885.

to have associative connections with the anterior portions, they are located posterior to the cerebellum. The inhibitory influences noticed especially during the first two or three days after the operation, I attribute to the loss of association fibers. The centers for swallowing, the sense of equilibrium, and heart action seem to have only slight associative connections with these anterior parts. It appears that the greater portion of the functions performed exclusively and in a more specialized degree by the cerebellum of the dog is performed by the anterior third of the medulla of the frog. It was interesting to note after unilateral excision of the medulla, that the abnormal position of the spine and the rotatory movements were closely related in time of appearance, and also that the position of the body and legs were closely related to one another and to the two former phenomena. The rotatory movement around the sagittal axis was the first phenomenon to appear and also to disappear, whereas the sensory ataxia and the atonia became apparent only when the forced rotatory movements became less vigorous. I attribute the forced rotatory movements principally to the direct acute disturbance caused by the excision of an important component of the neuron-complex pertaining to the geotropic sense. The fading away of the forced rotatory movements accordingly would mark the disappearance of this acute disturbance owing to the function vicariously assumed by paths formed by the union of the intact neurons of the broken neuron-complex with other neurons surrounding them. When these new paths were fully formed and the acute symptoms had in part subsided, the atonia and sensory ataxia became more prominent.

The absence of abdominal respiratory movements on the homonymous side after unilateral medullar excision anterior to the calamus scriptorius proves that the centre for abdominal respiration is present in the medulla above the calamus and that its centrifugal fibers do not appreciably cross, moreover, that it does not control the laryngeal and narial respiratory movements, since these still persist bilaterally and normally. The loss of the eye reflex to pressure on the homonymous side is to

be attributed to the excision of the origin or section of the fifth, the sympathetic, or the third nerve, or of all three. This phenomenon also proves that these nerves do not appreciably cross. I attribute the upward and outward position of the crossed eye to the fact that its superior oblique muscle is no longer innervated, since the nervus trochlearis crosses, and its nucleus, as well as the nuclei of all the nerves that govern the muscles of the eye on the operated side have been excised in the operation. Consequently, the superior oblique is the only muscle of the eye on the operated side that is still innervated and this fact explains the downward and upward position of the homonymous eye. Since this eye was covered by the nictitating membrane, it is evident that the downward movement of the eye is correlated with upward movements of the nictitating membrane. The persistence of the swallowing and croak reflex after unilateral medullar excision, shows that these are bilaterally quite independent in the frog and that one side may perform the function. This operation in conjunction with operation XVII proves that the sense of equilibrium is lost when the origin of the eighth nerve is destroyed.

The unilateral excision of the medulla anterior to the origin of the vagus group, in conjunction with the unilateral excision of the medulla posterior to the origin of this group, adds the fact that as long as the origin of the vagus group is intact, abdominal respiratory movements persist on the homonymous side. It is apparently easier to injure abdominal respiration by excisions posterior to the external origin of the vagus group, than anterior to its origin, owing probably to the fact that the deep origin of this group is more posterior than anterior to the external origin. The contracted pupil of the homonymous eye, noted after unilateral excision of the medulla posterior to the origin of the vagus group, was probably due to the destruction of the path of the sympathetic.

Unilateral excision of the middle third of the medulla in fishes, according to Hyde,[1] removes the ganglia for respiratory

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[1] Hyde, I. H. *American Journal of Physiology*, **10**, 5, 1904.

movements, namely those of the seventh, ninth, and tenth nerves, and indicates that the narial and oral respiratory apparatus innervated by the seventh and ninth, can continue their respiratory movements independently of those of the abdominal; moreover, that no appreciable crossing of the efferent fibers of these ganglia takes place. Furthermore, it corroborates the result found after unilateral excision of the medulla, namely, that the croak ganglia are located in the origin of the vagus group and are functionally independent, although probably closely connected with one another by association fibers.

The excision of everything anterior to the spinal cord corroborates a multitude of facts found in previous operations, and proves that co-ordinated movements do not cease with the removal of all the nervous structures anterior to the spinal cord. It moreover shows that apparently some inhibitory influence is taken away from the spinal cord with the removal of the structures anterior to it.

My experimental results on the medulla agree with SCHRADER[1], who states that frogs cease to catch flies if the optic thalami are injured; that the reactions on the rotating table are reflex in character, the stimulations acting upon the semicircular canals and passing to the centre by the acoustic nerve; that frogs with injured medulla show a loose position of the feet when resting, and that their heads point toward the ground. Furthermore, that the medulla, down to the calamus scriptorius may be removed in the frog without destroying co-ordinated movements and that centres for respiratory movements, swallowing and croaking are in the medulla. My observations also corroborate SCHRADER's statement that after lesion behind the vagus group there is often complete inversion of the stomach and oesophagus, accompanied by prolapsus into the mouth, and that the frog after section of the medulla even behind the trigeminus group is still able to turn over on the ventrum when placed on its dorsum. SCHRADER also states that if the section

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[1] SCHRADER, M. *Pflüger's Archiv*, **41**, 75, 1887.

is behind the trigeminus group and if the brain anterior to this group is removed, every reaction on the turning table ceases.

The excision of everything anterior to and including the greater part of the brachial plexus, proves, as SCHRADER observed, that co-ordinated movements stop only because the origin of the nerves of the front legs is destroyed ; that after removal of the medulla, co-ordinated movements still remain, and that the more nearer the section approaches the origin of the brachial plexus, the more is co-ordination impaired.

TABLE OF OPERATIONS AND CHIEF RESULTS.

I. Excision of one cerebral hemisphere.
  (a) During the first three days the animal jumps slightly toward the crossed side.
  (b) From four days to two and a half months, no deficiencies were noticed.
II. Excision of both cerebral hemispheres.
  (a) During the first three days, bilateral slightly defective strength of the muscles and somewhat subnormal skin reflexes.
  (b) Later, to two and a half months, no deficiencies were observed.
III. Unilateral removal of the thalamus.
  (a) During the first two weeks,
    (1) Voluntary movements rare.
    (2) Touch sensibility very defective.
    (3) Almost total blindness on the crossed side.
    (4) Crossed legs are weaker.
  (b) From three weeks to two and a half months afterwards, (1), (2), and (4) are slightly, but (3) is not at all improved.
IV. Bilateral removal of the thalami optici,
  Causes these permanent deficiencies :
    (1) Almost complete bilateral blindness.
    (2) Touch sensibility very much impaired.
    (3) Voluntary movements very rare.
V. Unilateral removal of the lobus and thalamus causes,
  (a) From one half hour to two weeks,
    (1) Total loss of sight on the crossed side.
    (2) Forced straight-ahead movements.
    (3) Abnormal retention of urine.
    (4) Reduction in voluntary movements and touch-sensibility.
  (b) From third week to two and a half months, (1) is unimproved, (2) is much improved unless the animal is excited, (3) is normal, and (4) somewhat improved.
VI. Bilateral removal of the lobi and thalami.
  (a) From one half hour to three weeks,
    (1) Total blindness on both sides.

    (2) Other symptoms as noted under operation V, but in a more marked degree.

  (b) From three weeks to two and a half months, (1) remains unimproved, (2) normal, (3) other symptoms as noted under operation V (b).

VII. Unilateral removal of the lobus opticus.

  (a) From one half hour to two weeks,

    (1) Trifling defect in sight on crossed side.

    (2) Forced straight-ahead movements and abnormal urine retention as noted after operation V (a).

  (b) From two weeks to two and a half months,

    (1) Sight is normal.

    (2) The other two symptoms as indicated in operation V (b).

VIII. Removal of both lobi optici.

  (a) From one half hour to two weeks,

    (1) Trifling bilateral defect in sight.

    (2) The other symptoms as noted under operation VII (a), but stronger.

  (b) From two weeks to two and a half months,

    (1) Sight is normal on both sides.

    (2) The other symptoms as noted under operation VII (b).

IX. Removal of the anterior half of the lobi optici.

  (a) From one half hour to two weeks,

    (1) The same symptoms as after operation VIII (a), excepting that the forced movements were absent.

  (b) Later, to two and a half months, the animal showed nothing abnormal.

X. Removal of the posterior half of the lobi optici,

  (a) From one half hour to two weeks, forced straight-ahead movements.

  (b) Later, to two and a half months, the forced movements are present only when the animal is much excited.

XI. Removal of both thalami optici and the anterior half of the lobi optici.

    All symptoms are noted under operation VI excepting that the forced movements were absent.

XII. Removal of the dorsal half of both thalami and lobi optici.

    All symptoms as noted under operation VI but in a lesser degree, whereas sight was only slightly and temporarily (two weeks) affected.

XIII. Bilateral removal of the cerebellum.

  (a) From a half hour to three weeks,

    (1) Flat position of the frog.

    (2) Jumps infrequent, weak, and unsteady.

  (b) Later, to two and a half months,

    Muscular weakness and unsteadiness is marked only when the frog is excited ; the animal is unable to catch flies, although it sees them.

XIV. Unilateral removal of the cerebellum.

  (a) From a half hour to one week,

    (1) Limbs of crossed side, especially the posterior one was abnormally far extended and abducted.

    (2) Locomotion is always toward the homonymous side.

    (3) Head was lower and almost touched the ground on the homonymous side.

(4) Spine was bent in the thoracic region concave to the homonymous side.

(b) From second week to two and a half months,

    (1) Locomotion improved very little.

    (2) All the other symptoms had considerably improved in one week; but were far from normal, and were characteristically present after stimulation two and a half months afterward.

XV. Bilateral excision of everything anterior to the medulla.

  (a) From a half hour to three days,

    (1) Croak reflex is difficult to elicit.

    (2) Turning over reflex is inhibited.

    (3) In addition, all symptoms as after operation VI and XIII.

  (b) Four days to one month after operation,

    (1) Collective symptoms of operation VI and XIII.

    (2) Croak and turn-over reflex are normal.

    (3) Swallowing, heart action and respiratory reflexes, and sense of equilibrium are intact.

XVI. Unilateral Excision of the right side of the medulla anterior to the calamus scriptorius.

  The observations pertaining to this operation necessitate recording at shorter intervals. I shall use the same number for an observation throughout, and after noting a phenomenon once, shall not mention it again until at the end, unless it changes.

  A. Ten minutes after operating.

    (1) No reaction with head or body movements on rotating table.

    (2) Body, especially anterior portion and head, are lower on homonymous side than on crossed side.

    (3) Legs on crossed side, especially the posterior one, are far extended and abducted.

    (4) Legs on homonymous side, especially anterior, are superflexed and adducted.

    (5) Forced rotatory movements around the sagittal axis of body toward the homonymous side are the sole movements.

    (6) Abdominal respiration on the homonymous side is stopped.

    (7) Narial and oral respiratory movements are bilaterally normal.

  B. One half to five hours after operating.

    (8) Eye reflex to pressure on the homonymous side is gone but is normal on the crossed side.

    (9) Crossed eye is turned upward and outward.

    (10) Homonymous eye is turned downward and inward.

    (11) Homonymous eye is turned upward synchronously with inspiration; and downward with expiration.

    (12) Nictitating membrane of homonymous eye is evidently beyond the animal's control; it covers the eye, especially when this moves downward.

    (13) Croak reflex elicited only in a depressed degree.

    (14) Swallowing reflex is normal.

    (15) Spine and neck curved as after operation XIV.

(16) Tremor on both sides; but strongest on the homonymous side.

(17) Weakness of muscles in proportion to tremor.

(18) Sight is perfect on both sides,

C. Twenty-four hours after operating.

(1a) Rotating the table in clockwise direction, i. e., toward the operated side, the frog moves his head in anti-clockwise direction; after rotating, the head is brought back beyond the sagittal axis of the body in clockwise direction.

(1b) Rotating in anti-clockwise direction elicits no head movements; but a slight, circular movement of the body in an anti-clockwise direction is noted after rotating the table.

(5) Is increased by the slightest stimulation.

D. Two days after operating,

(1a) Same as after one day but in addition, sometimes a circular movement of the body in clockwise direction after rotating the table.

(1b) Same as after one day.

(5) Diminishing.

E. Three days after operating,

(2), (3), and (4) were temporarily normal during short intervals while the frog was resting.

F. Five days after operating,

(5) Frog rotates only when it attempts to jump.

G. Six days after operating,

(5) Frog, on jumping, sometimes lands on dorsum.

H. Ten days after operating,

(13) Is normal.

(1), (1), (3), and (4) are still far from normal.

(5) On jumping, frog sometimes lands on dorsum and sometimes on homonymous side.

I. No appreciable change in any symptoms from tenth to fifteenth day.

XVII. Unilateral excision of the right side of the medulla anterior to the origin of the vagus group.

(a) The same phenomena as observed after operation XVI; excepting that

(b) Abdominal respiration is intact on both sides.

(c) The croak reflex is normal immediately after the operation.

(d) The bilateral apnoeic pauses in abdominal respiration, after rotating movements around the sagittal axis, are pronounced.

XVIII. Unilateral excision of the right side of the medulla posterior to the origin of the vagus group to the calamus scriptorius.

Causes from first to fifteenth day—

(1) Slight impairment of the abdominal respiration on the homonymous side.

(2) Contraction of pupil on the homonymous side.

(3) Weakness of limbs on the homonymous side.

(4) Position of legs, body and head as observed after operation XVI, but in a lesser degree. They improved during the first week but did not regain normal.

XIX.   Unilateral excision of the right middle third of the medulla including the origin of the vagus group.

    (a) Phenomena which showed no change from first to the fifteenth day—

        (1) Abdominal respiration on the homonymous side is completely abolished.

        (2) Pupil of this side is contracted.

    (b) Phenomina as observed after operation XVIII,

        (1) Position of head, legs, and body.

        (2) Defect in locomotion.

XX.   Bilateral excision of the middle third of the medulla, including the origin of the vagus group.

    (a) Abdominal respiration is abolished on both sides, also, the croak, turn-over, and swallowing reflex is gone.

    (b) The head points into the ground.

    (c) Urostylic prominence is gone.

    (d) Complete inversion of oesophagus and stomach with prolapsus outside of the mouth.

    (e) Heart becomes feeble two hours after operating.

    (f) Eight hours after operating, respiration of nares and mouth is exaggerated, due to asphyxia.

    (g) Frogs died 8 hours after operating.

XXI.   Excision of everything anterior to the spinal cord.

    (a) Respiratory, croak, swallowing, heart-action, and turn-over reflexes are gone entirely.

    (b) Sense of equilibrium is lost.

    (c) Eye reflex and sight is lost.

    (d) Stimuli are answered sooner and with greater certainty than when higher portions of the brain are intact.

    (e) Heart action gradually ebbs away during the five hours which the frog usually lives after the operation.

XXII.   Excision of everything anterior to and including the anterior portion of the spinal cord almost down to the origin of the brachial plexus.

    (a) All phenomena of operation XXI.

    (b) Co-ordinated movements fade away during the first two to three hours after this operation.

    (c) Three hours after operating, the fore limbs cannot support the body any more.

    (d) The frog is usually dead five hours after the operation.

THE CENTRAL GUSTATORY PATHS IN THE BRAINS

OF BONY FISHES.

By C. Judson Herrick.

Studies from the Neurological Laboratory of Denison University. No. XVIII[1].

With Forty Figures in the Text.

CONTENTS.

Section I.   Introduction.

The conception of the nervous system as a mechanism for putting the organism into correspondence with the external environment and, in higher animals, for coordinating the reacting apparatus itself (internal environment) may be said to give the key to its evolutionary history.   These two factors have given direction to the differentiation of the nervous system into somatic and visceral systems respectively and the further subdivision of each of these.

The labors of the students of nerve components have given us for the peripheral nervous system a paradigm or schema which seems to hold for all vertebrates, though with infinite variation in its details ; and it now remains to correlate these peripheral components with the central conduction paths so as to give a detailed knowledge of the whole course of each reflex pathway.

In attacking this general problem there are obviously two general lines of procedure open to us :—(1) beginning with the simplest brains we may work out exhaustively for each critical species in the phylogenetic series the conduction paths as completely as possible by monographic treatment of types and thus in the end approximate to a reconstruction of the phyletic history of the nervous system. (2) Or we may take each sensori-motor reflex system as the unit and trace its phylogeny through the series of types. This second method has the obvious advantage that one can start with the system in question in some type where it attains maximum develop-ment and, having arrived at a thorough knowledge of its anato-my and physiology here, it will be easier to read this schema backwards to the more primitive animals, as well as forwards in its further evolutionary modifications. It is hardly necessary to call attention to the fact that the human nervous system is the least favorable starting point for this sort of a research ex-cept for the neo-pallium and its appendages.

Each method has its advantages. The monographic treat-ment of type brains is really far more difficult, even in the low-est vertebrates, because of the difficulty in interpreting such simple undifferentiated pictures and analyzing a complex where there are few salient features. But nature has effected the analysis for us in some of the more specialized types by the hypertrophy of isolated systems ; and if, as sometimes happens, the other functional systems are in a primitive or reduced con-dition, we have a favorable point of approach for a monographic study of the exaggerated functional system (cf. Judson Her-rick, '03).

The purpose of this study is to make such a detailed analy-

sis of a single functional system of neurones—the gustatory system—in types where it reaches its maximum development and is obscured as little as possible by a high development of other systems. These conditions are fulfilled perfectly in the cyprinoid and siluroid fishes, whose brains are uncomplicated by any pathways leading to or from the cortex of the fore-brain and are in the main merely reflex mechanisms, but whose peripheral gustatory pathways are more highly developed than in any other vertebrates.

Section II. The Peripheral Gustatory System in Fishes.

As is well known, taste buds occur freely scattered over the mucous lining of the mouth and gills of nearly all fishes from the lips to the oesophagus. These are innervated by the VII, IX, and X cranial nerves. Similar taste buds, commonly called terminal buds, occur in the outer skin of some fishes and these also have been recently shown to be gustatory in function (Judson Herrick, '04). They are, in all cases where the innervation is known, supplied by the facial nerve. All taste buds in the pharynx and back part of the mouth, then, are supplied from the vagus and glossopharyngeus, those in the front part of the mouth, lips and outer skin from a root of the facialis which apparently corresponds with the portio intermedia of human anatomy.

Associated with each of these roots are unspecialized visceral sensory fibers ending by free arborizations in the mucous membrane of the mouth cavity, these being very numerous in the region of the lower vagal roots and diminishing cephalad. The central connections of these two elements have not as yet been clearly differentiated, and both are provisionally designated the " communis system " of nerves by students of nerve components. With the unspecialized fibers we are not here concerned. The specialized communis fibers related with taste buds, either within or outside the mouth, and the ganglion cells from which they are derived will be termed the *peripheral gustatory system of neurones.*

The peripheral gustatory system has recently been worked up both anatomically and physiologically in a number of fishes, most thoroughly in the siluroids, or cat fishes (JUDSON HERRICK, 'o1 and '04). From the paper last cited we copy the accompanying figure (Fig. 1), which gives the peripheral distribution of the cutaneous branches of the communis root of the facial nerve to supply the taste buds in the outer skin, in the horned pout, Ameiurus.
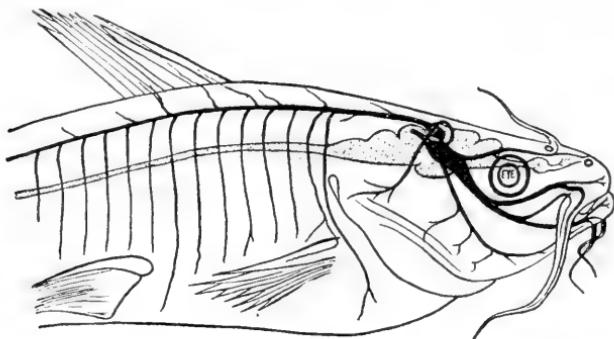
Fig. 1. A projection of the cutaneous branches of the communis root of the right facial nerve in *Ameiurus melas*, Jordan and Cope. Natural size.

The branches of this nerve which supply taste buds within the mouth are not drawn. All of the branches shown are gustatory in function. From the *Bulletin of the U. S. Fish Commission* for 1902 (JUDSON HERRICK, '04).

The general form of these buds of Ameiurus and their relations to the skin are shown in Figure 2. Practically all parts of the skin in these fishes are provided with taste buds supplied by this root, these same areas receiving also general cutaneous nerves for tactile sensation from other nerve roots, and the barblets being especially richly supplied with both sorts of nerve endings.

It has been determined by an experimental study of a series of both fresh water and marine fishes (JUDSON HERRICK, '04) that the cutaneous communis nerves are gustatory in function and that this function is absent from the skin in species where these nerves and their sense organs are not developed. When edible substances or sapid solutions were brought in contact with these cutaneous sense organs the fishes would react by the

appropriate movements to approach and seize the food and in
the case of the horned pout, Ameiurus, it was found possible to
differentiate a gustatory reaction from a tactile reaction and to
prove that both senses possess a "local sign ;" i. e., both the
tactile and the gustatory reaction can be localized in space.
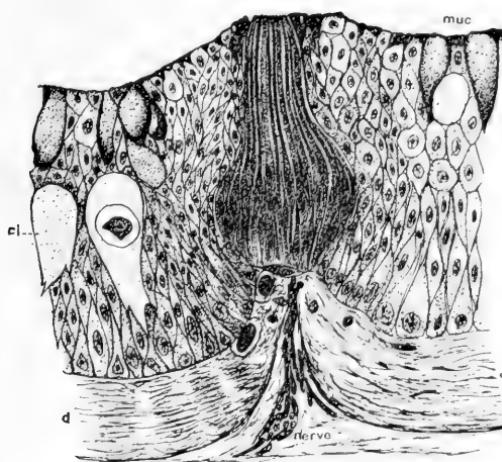
Fig. 2. Section through the skin of the top of the head of *Amiurus melas*,
showing a terminal bud. From the *Journal of Comparative Neurology.* (JUDSON
HERRICK, '01).

At *d* is the dermis which is raised into a low papilla under the sense organ
and whose center is pierced by the nerve for the organ ; *cl.*, clavate cells of
LEYDIG ; *muc.*, mucus cells of the epidermis.

The peripheral pathways for these motor responses are now
well known and the problem of the present research may be
thus stated : Given the terminal relations of the peripheral
gustatory neurones and the peripheral motor neurones involved
in the known gustatory reflex movements of these fishes, what
are the central connections between them ?

Experiment has shown that the taste buds in the outer skin
function in substantially the same way as those within the
mouth, though there are certain obvious differences, particularly
the fact that the stimulus if applied to the cutaneous taste buds

usually calls forth a movement of the whole body toward the food object, while this is unnecessary in the case of a gustatory stimulus received within the mouth. This is the probable reason for the differentiation of a special center in the medulla oblongata for the reception of the facial root of the communis system, the lobus facialis, or "tuberculum impar," in those species which possess large numbers of terminal buds in the outer skin.
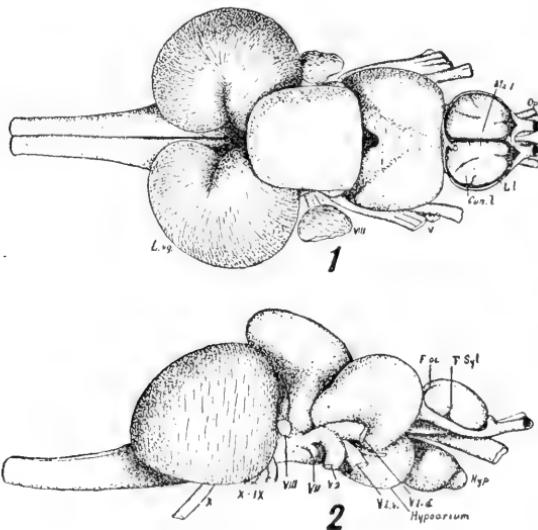
Fig. 3. Two views of the brain of the buffalo fish, *Carpiodes velifer* (Raf.), (1) from above, (2) from the right side. × 2. After C. L. HERRICK.
The vagal lobes (*L. vg.*) are relatively larger than in the carp and, with the overhanging cerebellum, completely conceal the facial lobe. In the lower figure the branches of the trigemino-facial root complex are marked *VI.d.*, *VI.v.*, *V2*, *VII*, and the root of the auditory nerve *VIII*. Between the latter and the caudal tip of the optic lobe is a well-defined protuberance ventrally of the cerebellum. This is the lateral portion of the superior secondary gustatory nucleus (*Rindenknoten*, MAYSER). Caudad of this, immediately dorsally of the VIII root, is the small lobus lineae lateralis (JOHNSTON) from which the tuberculum acusticum and cerebellar crest extend caudad beneath the vagal lobe. In the upper figure, the median shaded part of the roof of the optocoele is membranous, the optic lobes being widely divaricated by the enormous valvula cerebelli. In both figures the membranous roof of the fore-brain is dissected away to show the lobules of the basal ganglia, and the olfactory bulbs are cut away.

With the exception just noted, it is probably safe to assume that there will be found broad lines of similarity between

both the peripheral and the central gustatory paths in all verte-
brate types and that fishes like the carp with enormous hyper-
trophy of the gustatory roots of the VII, IX and X nerves may
safely be used as guides to point the way for further researches
upon the gustatory paths of higher vertebrates where the sys-
tem is less easily analyzed. Such being the case, our problem
assumes a measure of importance when we remember that the
central gustatory pathway is at present almost totally unknown
in all vertebrates, including man, and that even the peripheral
pathway is still in dispute among students of human anatomy.

It has been already pointed out (JUDSON HERRICK, '04)
that the siluroids (cat fishes and horned pouts) and the larger
cyprinoids (carps, suckers, etc.) present a striking similarity to
each other and contrast to other teleosts in both the peripheral
and the central nervous systems, and that these features center
about the gustatory pathways. In teleosts generally the gusta-
tory pathway from the lining of the mouth in the branchial re-
gion, entering the brain by the communis roots of the IX and
X nerves, and the gustatory pathway from the anterior part of
the mouth and from the outer skin, entering by the communis
VII root, terminate together in a single cerebral enlargement,
the lobus vagi. But in these two groups of fishes we have a
second tuberosity, as mentioned above, developed for the com-
munis root of the facialis to provide for the unusually large
number of taste buds in the outer skin supplied by this nerve.

In the cyprinoids, particularly the carp-like forms, both of
these lobes are enlarged, correlated with a high development of
the taste buds in each of the corresponding peripheral regions,
but particularly in the vagal region to supply the remarkable
collection of taste buds on the palatal organ. In the siluroids,
on the other hand, there is no hypertrophy of the gustatory or-
gans in the branchial region and the vagal lobes, accordingly,
are essentially similar to those of other teleosts. But the highly
developed cutaneous gustatory organs innervated by the facialis
have called forth an enlargement of the facial lobe greater than
that of cyprinoids. Since in the siluroids all of the taste buds
of the outer skin are supplied by the communis root of the

facialis (JUDSON HERRICK, '01) and since the palatal and other branches of the communis VII root which supply taste buds within the mouth are not enlarged, as compared with other fishes, it is clear that the enormous communis VII root and the lobus facialis in which it terminates are related mainly to cutaneous taste buds in these fishes.
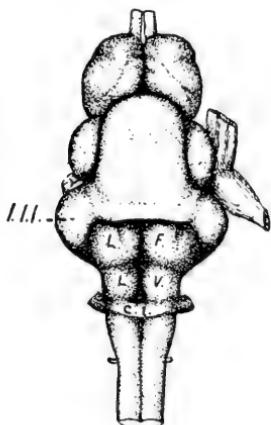
Fig. 4. Dorsal view of the brain of the yellow cat fish, *Leptops olivaris* (Raf.), $\times$ 2.

The olfactory bulbs are cut off; also the membranous roof of the fourth ventricle, exposing the facial lobes (*L. F.*) and vagal lobes (*L. V.*). This ventricle is bounded behind by a transverse ridge containing the commissura infima HALLERI (*c. i.*) and the commissural nucleus of CAJAL. The tuberosity laterally of the cerebellum and facial lobe is the lobus lineae lateralis (*l. l. l.*), which is greatly enlarged and entirely conceals the superior secondary gustatory nucleus.

SECTION III. THE CENTRAL GUSTATORY SYSTEM OF CYPRINOID FISHES.

We shall now proceed with a description of the gustatory pathways in a selected series of teleosts, beginning with the larger cyprinoids where it attains its maximum development. The results here obtained will be controlled by an equally careful examination of the brains of siluroid fishes (particularly Ameiurus), whose gustatory centers differ greatly in detail from those of the carp-like forms. These minor differences will serve to bring out more clearly the points of fundamental resemblance, which are very striking.

The end-station of the gustatory neurones of the first order (peripheral neurones) is the nucleus of origin for the neurones of the second order, giving rise to secondary gustatory tracts, and these in turn to tertiary tracts. The nomenclature of these tracts and centers offers almost insuperable difficulties and some new terms will have to be introduced and old ones more nar-

rowly defined. A summary of the nomenclature here employed
for the gustatory system of these fishes is given in tabular form
in Section V, to which frequent reference should be made.

1. Primary Gustatory Centers.

The general topography for the vagal and facial lobes of
cyprinoid fishes has often been described, and the reader is re-
ferred for the details to the classic paper of MAYSER ('82), and
also to the figures of BELA HALLER ('96), whose descriptions,
however, I do not in all things confirm. I have found little in
the extensive work of this author ('98) on the brains of Salmo
and Scyllium which sheds further light on the secondary con-
nections of the vagal lobe. However, I do not profess to have
mastered the contents of this unsystematic and obscure paper,
though I have dilligently studied it. Nor is there anything of
importance from our present point of view in the recent disser-
tation on the vagal lobes of cyprinoids by GROTH ('00), whose
purpose was merely to test the accuracy of some of HALLER'S
observations on nerve anastomoses in these fishes.

The vagal lobe of the cyprinoids, as compared with that of
the siluroids and the teleosts generally, represents an en-
largement of both the sensory and the motor centers of
the vagus and glossopharyngeus. This enlargement is corre-
lated with the development of the curious palatal organ in the
mouth of these fishes, the sensory fibers being derived from the
taste buds which cover the surface of this organ and the motor
fibers going out chiefly to the small muscles which permeate its
interior. The '' motor layer '' of the vagal lobe, from which
these motor fibers are derived is a dorsal extension of the nu-
cleus ambiguus. The latter nucleus has the typical position
and relations, supplying the branchial musculature, and is not
commonly regarded as a part of the vagal lobe.

We shall describe, so far as the material at command per-
mits, the conduction pathways in the vagal lobe of the larger
cyprinoids on the basis of sections of adult and young brains
cut in various planes and stained by DELAFIELD's haematoxylin
and the methods of WEIGERT-PAL and GOLGI. The illustrations

given throughout the remainder of this paper are all camera drawings of single sections, except Fig. 20, which is a composite, and the schemata, Figs. 38, 39 and 40.

First a few words by way of general orientation. The vagal and facial lobes are dorsal structures in the oblongata, but they do *not* represent, as commonly taught, the morphological continuation of the dorsal horns of the spinal cord. These are represented in the spinal V tract and its associated substantia gelatinosa Rolandi, their ventro-lateral position in the vagus region of these brains being due to crowding by the more mesially placed gustatory centers. The latter centers, therefore, if morphologically related to anything in the spinal cord, must represent spinal structures lying dorsally of the canalis centralis and beneath the floor of the dorsal fissure. In the oblongata this fissure opens out and its floor becomes greatly extended to form the membranous roof plate (His), or velum medullare posterior, *beneath* which the lobes in question are developed (cf. Judson Herrick, '99, p. 213).

Figure 5, taken midway of the vagal and facial lobes of the carp, illustrates how these structures are superposed upon the great longitudinal conduction paths which constitute the chief landmarks of morphological relationship. The spinal V tract, whose substantia gelatinosa at this level is reduced to a mere vestige, lies ventrally of both the sensory and motor vagus roots. Crowded into the space ordinarily occupied by the substantia gelatinosa Rolandi are the great longitudinal secondary gustatory paths, ascending and descending. Mesially of these is the substantia reticularis, shown by Cajal and others to be the continuation of the ventro-lateral funicle of the spinal cord and to be composed of short paths, mostly sensory fibers of the

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Fig. 5. A transverse section taken through the middle of the vagal and facial lobes of an adult carp stained by the method of Weigert-Pal. × 16.

The layers of the facial lobes and the vagus roots are designated at the right. *a. s. X.*, ascending secondary gustatory tract from the vagal lobe ; *com. r. VII*, communis (gustatory) root of the facialis entering the facial lobe ; *d. s. VII*, descending secondary gustatory tract from the facial lobe ; *lm.*, lemniscus (laterales Längsbündel, Mayser); *sp. V.* spinal root of the trigeminus.

superficial root.

secondary neurones

deep root

sec. gustatory tract

motor layer

deep root

motor root
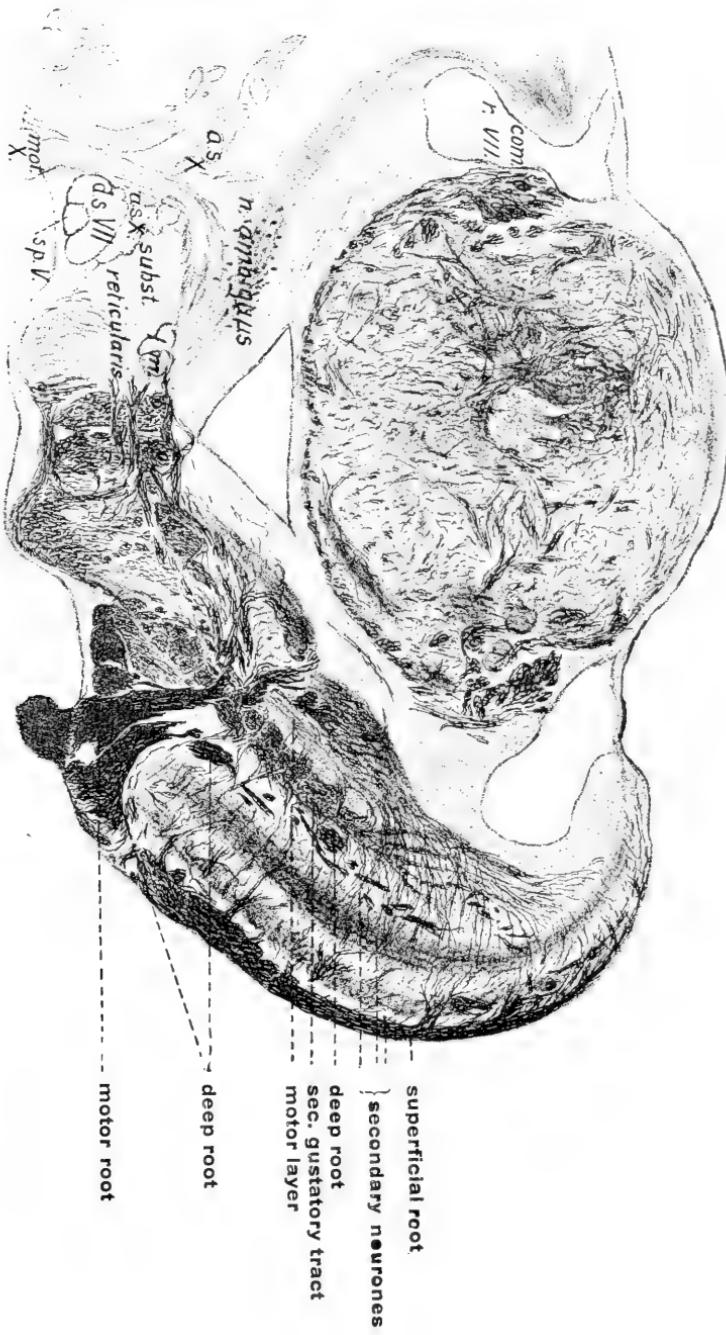
third order designed to distribute sensory excitations over a large field of motor nuclei of the oblongata. Close to the raphé in the median line is the fasciculus longitudinalis medialis, likewise composed largely of short paths and chiefly motor. Between this fasciculus and the substantia reticularis, there is ventrally the continuation of the ventral funicle of the spinal cord and dorsally the lemniscus (funiculus lateralis, FRITSCH; laterales Längsbündel, STIEDA and MAYSER).

The *lemniscus* is very complex. It clearly is composed in the main of crossed ascending fibers from the primary sensory centers of the spinal cord and oblongata to the mid-brain. These fibers correspond closely with the lemniscus lateralis or lateral fillet of mammals. The lemniscus medialis, or direct pathway to the cerebral cortex, as found in mammals, is of course not present here and this whole ascending path I shall term simply lemniscus. It probably receives fibers from the whole length of the spinal cord with a large accession of similar fibers from the funicular nuclei and enormous numbers of fibers from the tuberculum acusticum. It receives no appreciable number of fibers from the vagal lobes or other visceral sensory centers and therefore may be considered a somatic sensory secondary tract. It terminates in the mid-brain beneath the tectum in the protuberance into the optocoele which is so characteristic of the teleosts and is termed the torus semicircularis (nucleus lateralis mesencephali, EDINGER). This body, in fact, seems to be primarily the end-nucleus of this tract. Whether this bundle also contains descending fibers I do not know, but am sure that if present they are relatively few in teleosts. Such descending fibers would of course have to be excluded from the designation lemniscus.[1]

Some of the smaller cyprinoids (e. g., Notropis) exhibit but little enlargement of the vagal lobes. In the gold fish (*Carassius auratus*) the vagal lobe is greatly enlarged, but the

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[1] The reader will note that this tract is designated *lemniscus* on account of its partial homology with the tract of that name in the mammals, and that it has nothing to do with the so-called lemniscus of MAYSER and others, or tractus tecto-bulbaris et spinalis.

sensory roots of the IX and X nerves penetrate at once to its deeper layers and then turn outward to end near the surface much as will be described in Ameiurus. In Cycleptus the lobe is larger and the sensory roots penetrate but little before they spread out to end in a superficial layer of large cells which stain very pale in haematoxylin. And in the carp (Fig. 5), whose vagal lobes are still more enlarged, the greater part of the sensory roots do not penetrate, but spread out over the whole outer surface of the lobe (constituting MAYSER's first layer), thence to pass in separate strands directly into a thick layer exhibiting alternate bands of crowded small cells and dense neuropil (MAYSER's second layer).

This will be termed the *layer of secondary neurones.* Sections stained by DELAFIELD's haematoxylin show within it seven concentric bands of cells and neuropil which are more or less sharply distinguishable, of which the two outer are of greatest importance. The first is a thin layer of crowded cells of relatively large size which take up a very pale stain—the chief secondary gustatory neurones. Immediately internal to and among these cells are smaller very closely crowded cells whose nuclei take up a very intense stain. These will be termed the smaller gustatory neurones. The other bands contain chiefly minute cells with deeply staining nuclei and occasionally larger, irregularly shaped cells among them, while the inner border of this layer is a band of neuropil containing a few large cells which take a very pale stain. Sections stained by the method of PAL show sensory root fibers entering this band at its inner border. These root fibers will be termed the deep communis root of the vagus, as distinguished from the larger superficial root (Fig. 5). The fibers of the deep root turn outward to end in the second layer along with those of the superficial root.

This layer of secondary neurones is very wide in Cyprinus and is traversed radially by unmedullated and delicately medullated fibers for the deeper layers of the vagal lobe. The large pale cells forming its outer boundary are the most important and characteristic cells of the lobe, for they give rise to the

great secondary gustatory tracts which leave the lobe for distant centers. The narrow layer of smaller cells adjacent to these may share this function, but their neurites are mostly shorter. The small cells of the other bands of this layer have short neurites which terminate for the most part within the lobe and are therefore called intrinsic secondary gustatory neurones.

Immediately internal to the seventh band of the layer of secondary neurones is MAYSER's third layer, the *layer of secondary gustatory fibers*, which pass ventrally to constitute the "secondary vagus bundle" of MAYSER. These fibers are of small caliber with thin sheaths which take a very pale stain by the WEIGERT method.

Internally from the secondary gustatory tract is the *motor layer* (MAYSER's fourth), containing large cells which give rise to motor root fibers of the IX and X nerves. The thick ependyma containing large blood vessels is MAYSER's fifth layer. Some of its supporting elements are shown in Fig. 6.

The endings of the peripheral neurones which compose the superficial layer of root fibers of the vagal lobe of the cyprinoids are richly impregnated in many of my GOLGI preparations. Those of the deeper layers impregnate with much more difficulty. They are seen in Fig. 6. The superficial fibers end by extensive terminal arborizations which ramify widely among the dendrites of the chief secondary gustatory neurones, forming a very dense neuropil in the more superficial parts of the layer of secondary neurones, though some penetrate through the whole thickness of this layer. These endings are shown in Figs. 6 and 15 and somewhat imperfectly in Fig. 8. Fig. 6 shows that the slender strands of root fibers pass from the superficial to the deep layers of root fibers throughout the whole extent of the vagal lobe.

The most caudal fibers of the vagus constitute the descending or spinal root of this nerve, which passes a very short distance caudad to terminate in the grey centers associated with the commissura infima HALLERI and funicular nuclei as CAJAL ('96, p. 46) describes the endings of the fasciculus solitarius in the nucleus commissurale of the mouse.

The general arrangement of the *chief secondary neurones* may be understood by reference to Fig. 7, drawn from a sagittal section of a young carp, where these cells are richly impreg-
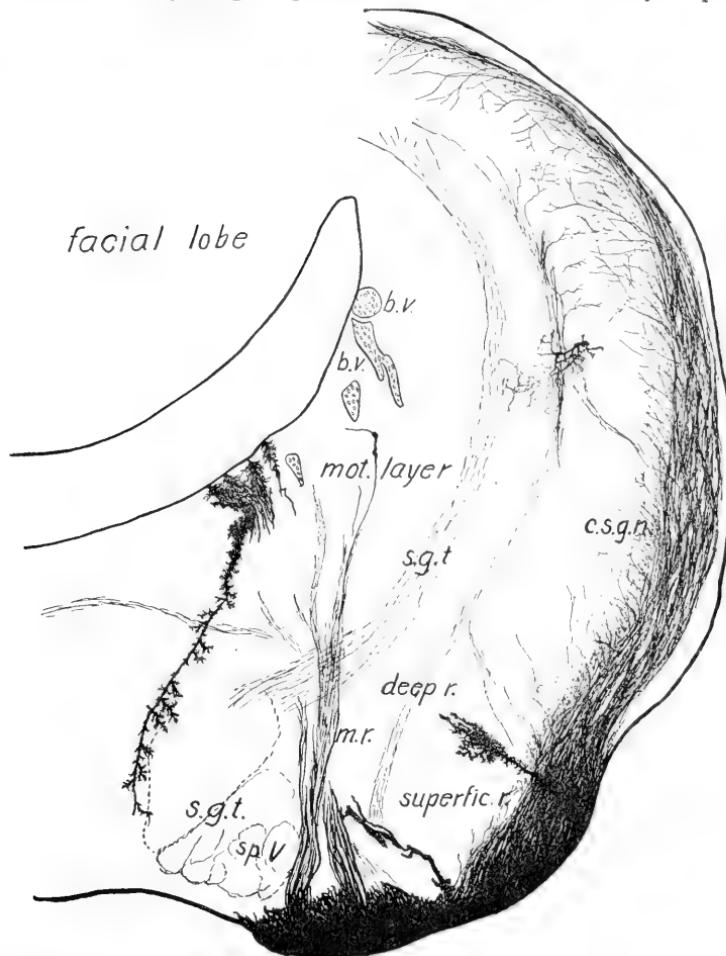
Fig. 6. Transection through the vagal lobe of *Catastomus commersoni.* GOLGI method. × 40.

The section illustrates the endings of the superficial and deep layers of root fibers of the vagus and the position of the chief secondary gustatory neurones (*c.s.g.n.*). An intrinsic neurone of type II is shown with dendrites in relation with the termini of the deep root. Two neuroglia cells of the superficial series are drawn and several of the deeper series (some of the latter having been drawn from an adjacent section). *b.v.*, blood vessel; *m.r.*, motor root of the vagus; *s.g.t.*, secondary gustatory tract; *sp. V*, spinal V tract.

nated. The layer of root fibers is not impregnated in this preparation, but its relations are suggested in Fig. 8 and more clearly in Fig. 6. In Fig. 8 root fibers are stained in the ventral part
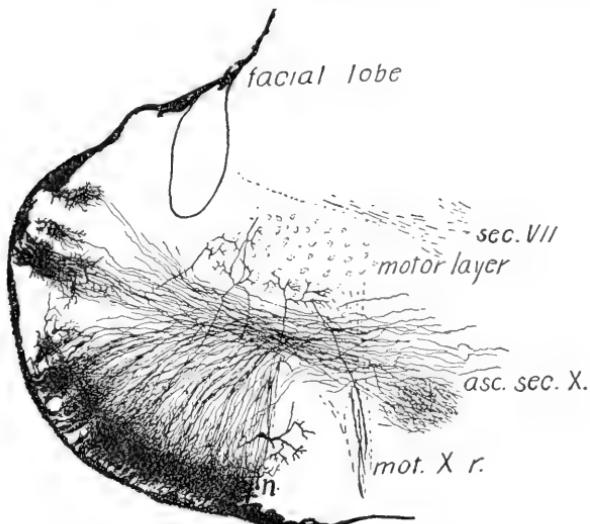
Fig 7. Section through the vagal lobe of a young carp, 5 cm. long. GOLGI method. × 40.

The section is approximately sagittal, but strongly inclined so that, while the caudal end (at the left of the figure) is near the median line, forward it passes toward the right. It includes, therefore, the motor nucleus of the right vagal lobe and the right side of the facial lobe, only the extreme caudo-ventral border of which is indicated. The preparation gives a typical view of the chief secondary gustatory neurones of the vagal lobe. One of the smaller secondary neurones (*n*) is shown at the extreme ventral (lower) side of the vagal lobe (cf. Fig. 11). A few scattered neurones of the deeper portions of the layer of secondary neurones are imperfectly impregnated. A few thick fibers are seen to pass from the layer of secondary neurones into the motor layer to arborize widely among its cells. Their origin could not be determined, but is probably from some of the deeper cells of the layer of secondary neurones. *Asc. sec. X.*, ascending secondary gustatory tract ; *mot. X r.*, motor root of the vagus.

of the vagal lobe, but only secondary neurones in its dorsal part. In preparations where both are impregnated together the peripheral layer of secondary neurones presents an indescribably intricate complex of interlacing fibers. Fig. 9 shows a single one of the chief secondary neurones of Fig. 8 drawn separately on a larger scale.

These neurones are densely crowded in radial arrangement over the entire periphery of the vagal lobe and are of very peculiar form. They are unipolar with irregularly elongated cell body and dendrite springing from the inner end. The
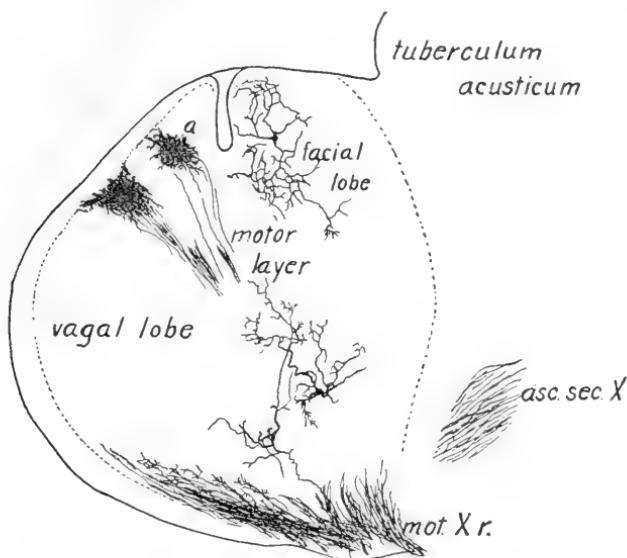
Fig. 8. Sagittal section through the vagal lobe of a young carp. GOLGI method. Drawn from the same series as Fig. 7, but farther toward the right side, so as to cut tangentially the extreme right borders of the vagal and facial lobes. ✕ 40.

The figure illustrates a few gustatory neurones of the vagal lobe and (imperfectly) endings of the gustatory root fibers, also two neurones of the deeper portion of the layer of secondary neurones whose processes reach the motor layer (cf. Fig. 7). These cells appear to be of the same type as the large cell lying in the layer of secondary tracts in Fig. 13. The neurone in the facial lobe is sketched in from the section lying next mesially, It occupies the area intermedia of the facial lobe and spreads out over the whole of the lateral aspect of the latter, its neurite not being shown. It is evidently of the same type as the one figured in Fig 18 at *a*.

peripheral end of the cell body is drawn out to a point which seems usually to reach the external limiting membrane of the vagal lobe. In these young fishes the external layer of root fibers is relatively thin. In older carp this layer is much thicker and there is no well defined external limiting membrane. The bushy dendrite breaks up at once into a very dense mass of

exceedingly fine branchlets among which the arborizations of the root fibers end. From one or more of the terminal branches of this dendrite a very delicate neurite arises and goes by the shortest path directly into the layer of secondary tracts by which it leaves the vagal lobe to enter the longitudinal secondary gustatory tracts of the oblongata, meanwhile taking up a

Fig. 9. A chief secondary gustatory neurone from the vagal lobe of the carp—the neurone designated *a* on Fig. 8. × 250. The black mass at the left of the neurone is precipitate deposited in the external limitating membrane of the vagal lobe.

very delicate medullary sheath. In its passage through the layer of secondary tracts it sometimes gives collaterals into the motor layer of the vagal lobe (Fig. 10).

Upon casual examination these chief neurones might suggest the appearance of neuroglia elements. The latter, however, are of totally different form (Fig. 6) and there is no opportunity for confusion. The gustatory neurones have exceedingly fine and densely branched dendrites, while the branches of the neuroglia are thicker and of the peculiar mossy or pulverulent appearance so characteristic of the supporting elements. The neuroglia, moreover, as a rule impregnates with a dark brown instead of black color.

Besides the chief gustatory neurones just described, there are closely associated with them just internally the smaller gustatory neurones shown in Figs. 11 and 12. These have the same general form and arrangement, but are much simpler. The cell body is smaller and usually rounded and the dendrite less profusely branched. The slender neurite arises from the tip of the dendrite and enters the layer of secondary tracts.

Some of these fibers or their collaterals enter directly the motor layer and there arborize. Others end by simple arborizations in the substantia reticularis and others turn caudad in the descending secondary communis tract. Whether any go cephalad
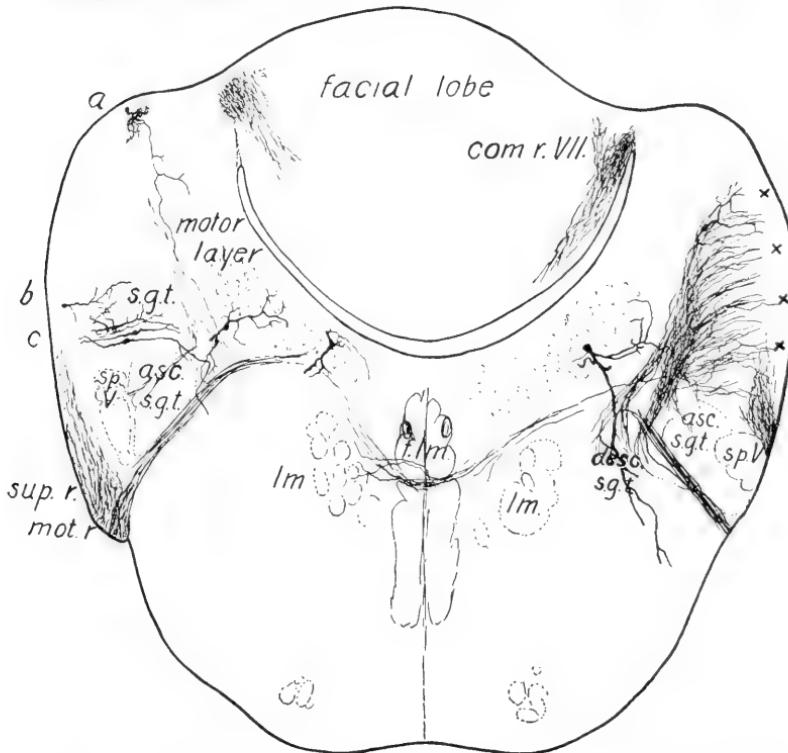
Fig. 10. Transverse section through the vagal and facial lobes of the spotted sucker, *Minytrema melanops* (Raf.) from a fish 8 cm. long. GOLGI method. × 40.

On the left at *a* a single chief secondary gustatory neurone is impregnated whose neurite sends collaterals into the dorsal part of the motor layer of the vagal lobe. On the right the area marked by the crosses is filled with a rich impregnation of similar cells which are not sketched in. At *b* is a single secondary neurone of the type shown in Fig. 12, and at *c* imperfect impregnations of deeper secondary neurones of the intrinsic type. On the right one cell of the motor layer is impregnated whose dendrites reach secondary gustatory tracts partly within the vagal lobe and partly in the substantia reticularis.

asc.s.g.t., ascending gustatory tract; *com.r.VII*, communis (gustatory) root of the facialis; *desc.s.g.t.*, descending secondary gustatory tract, entering substantia reticularis; *f.l.m.*, fasciculus longitudinalis medialis; *lm.*, lemniscus; *mot.r.*, motor root of the vagus; *s.g.t.*, secondary gustatory tract from the vagal lobe; *sp.V*, spinal V tract; *sup.r.*, superficial gustatory root of the vagus.

in the ascending secondary tract I have not determined.

These neurones clearly are of the same type as the chief gustatory neurones, but their neurites have a shorter course as a rule. Cells of this type in my preparations are impregnated chiefly in the more superficial parts of the layer of sec-
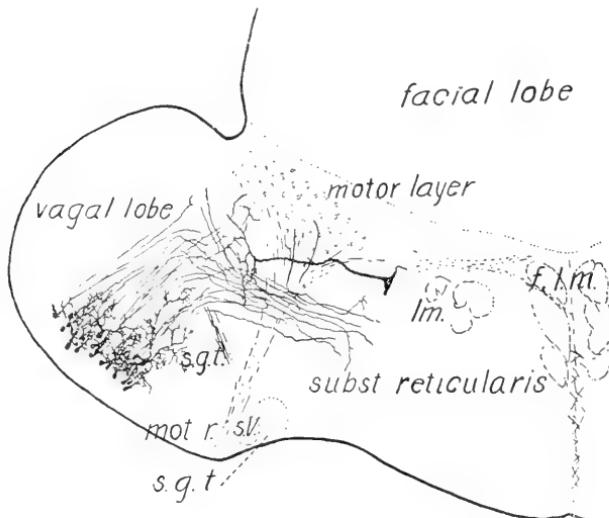
Fig. 11. Transverse section through the vagal and facial lobes of a young carp 5 cm. long. The section is obliquely inclined with the left side a little farther caudad than the right and the dorsal side much farther cephalad than the ventral. GOLGI method. × 40.

The section passes through the extreme cephalic end of the vagal lobe. None of the chief gustatory neurones are impregnated in this preparation, the superficial cells drawn being of the smaller variety. Among them are two intrinsic neurones of the vagal lobe. There is impregnated also a single large neurone in the dorsal part of the substantia reticularis one of whose dendrites reaches the layer of secondary gustatory tracts and whose neurite passes toward the ventral commissure.

f.l.m., fasciculus longitudinalis medialis ; *lm.*, lemniscus ; *mot.r.*, motor root of the vagus ; *s.g.t.*, secondary gustatory tract ; *s. V*, spinal V tract.

ondary neurones ; but sections stained with haematoxylin show very numerous nuclei of the same appearance throughout this layer and occasional GOLGI impregnations show that they are in fact scattered less freely throughout the thickness of the layer.

There are frequent impregnations, usually very imperfect, of larger cells of different kinds in the deeper parts of this layer,

as shown in Figs. 7, 8, 10 and 13 ; but I have not been able
to trace the connections of all these types of cells. There are
many indications that they reach the motor layer of the vagal
lobe (Fig. 14) and substantia reticularis of the oblongata imme-
diately below the vagal lobe. In most of these cases the
dendrites spread irregularly among the other cells of this layer

Fig. 12. A single neurone of the smaller gustatory type from the right
vagal lobe of the carp. Drawn from the same series as Fig. 11, two sections
farther caudad. GOLGI method. × 250.

The main axis of the dendrite is directly prolonged to form the neurite.
Terminal arborizations of the gustatory root fibers occur among these dendrites.
The broken line represents the outer border of the vagal lobe.

and the processes which penetrate the motor layer do not differ
essentially from the others. There is one type of cells, how-
ever, among these whose dendrites extend tangentially over a
very wide area (Fig. 16, *b* and Fig. 18, *b*). In one case (Fig.
13) a neurite from a cell was seen to enter the secondary gusta-
tory tract ; but its further course is unknown. Fig. 13 also
shows one of the smallest of these intrinsic cells whose thorny
dendrites are sharply contrasted to the very delicate much
branched neurite (neuropodium), giving the cell the character-
istic form of GOLGI's type II.

This is apparently the most frequent type of these intrinsic
cells, though the neurite is rarely impregnated in recognizable
form. Fig. 6 illustrates a different form of this type of cell,
with cell body and dendrites among the endings of the deep
layer of root fibers and neuropodium between this layer and the
layer of secondary tracts.

STANNIUS ('49, p. 82) has shown that mechanical stimula-
tion of the vagal lobe of the carp produces movements of the
intrinsic muscles of the palatal organ. Since the nucleus am-
biguus of the cyprinoids does not differ from that of other
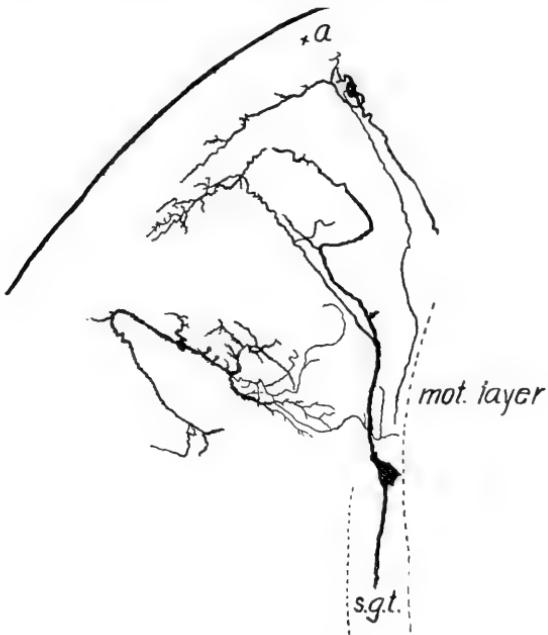
Fig. 13. Portion of the vagal lobe from a transverse section of the brain of
Minytrema melanops (Raf.) 8 cm. long. GOLGI method. × 187.

This is drawn from the same series as Fig. 10, the sections being adjacent.
For ease of orientation the position of the neurone marked *a* on Fig. 10 is desig-
nated *a* in this sketch. The large neurone at the bottom of the figure in the
layer of secondary gustatory tracts sends one of its two chief dendrites outward
into relation with the arborizations of the peripheral gustatory neurones, the other
is cut off. The neurite is not shown. The intrinsic neurone to the left of it is a
characteristic type II cell. The intrinsic neurone at the top of the figure is
drawn in from the adjacent section. Its neurite enters the secondary gustatory
tract (*s.g.t.*)

teleosts, in which it is known to innervate the branchial muscu-
lature, it is extremely probable that the cells of the motor layer
of the vagal lobe give rise to the nerve fibers for these intrinsic
muscles, for these two structures (the palatal organ and motor
layer of the vagal lobe) are always developed proportionately
with each other.

WEIGERT sections show very clearly that fibers of the motor roots of the vagus and glossopharyngeus arise not only from the nucleus ambiguus but also from the motor layer of the vagal lobe, as has been well known since MAYSER.

My GOLGI preparations very rarely show good impregnations either of the cells of the motor layer or of the nucleus ambiguus. The latter have the form and arrangement which have been often figured, the main dendrites spreading out in the substantia reticularis and reaching the extreme ventro-lateral border of the oblongata. Other smaller dendrites spread out within the nucleus itself and the neurite usually springs from the base of the main dendrite. The dendrites of the cells of the motor layer in some cases spread out within this layer, where they come into relation with the radial fibers which enter it from the layer of secondary neurones. Others reach out into the layer of secondary tracts and into the substantia reticularis (Fig 10), in both of which places they reach collaterals from the secondary gustatory tracts.

Fig. 14. Transverse section of the vagal lobe of the right side of a young carp, 5 cm. long. GOLGI method. × 50.

Illustrating two intrinsic secondary neurones of the vagal lobe whose processes extend inward to reach the motor layer. *s.g.t.*, secondary gustatory tract; *sp. V*, spinal V tract.

It appears that in no case do the peripheral motor neurones come into direct relation with the peripheral gustatory neurones, but at least one intermediary element is always interposed. These elements may be the intrinsic neurones of the vagal lobe, for short reflex arcs, or the chief secondary gustatory neurones for more complex reflex connections reaching beyond the vagal region of the brain.

The substantia reticularis is clearly the chief medium of communication between the sensory and motor centers for simple reflex paths here, as in higher vertebrates. This reticular substance receives gustatory fibers both from the secondary gustatory tracts and from the intrinsic neurones of the vagal lobe. We shall see beyond that it also receives fibers from the facial lobe.
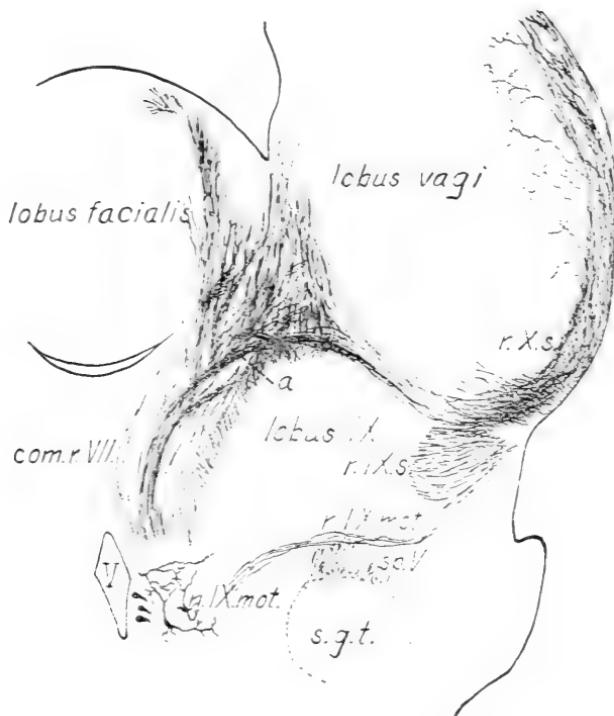
Fig. 15. Section through the right lobus glossopharyngei of a young carp 8 cm. long. GOLGI method. × 40.

The section is approximately transverse, but very oblique, so that the right side and the ventral surface are much farther cephalad. It cuts the lobus IX at its widest part and shows a strand of the communis root of the facialis (*a*) arching over its dorsal side and apparently entering both this lobe and the cephalic part of the lobus vagi. Terminal arborizations of the communis root of the vagus are also shown ending in the layer of secondary neurones of the lobus vagi.

com.r. VII, communis (gustatory) root of the facialis; *n.IX.mot.*, motor nucleus of the IX nerve; *r.IX.mot.*, motor root of the IX nerve; *r.IX.s.*, sensory root of the IX nerve; *r.X.s.*, superficial gustatory vagus root; *s.g.t.*, secondary gustatory tract; *sp.V*, spinal V tract; *V*, ventricle.
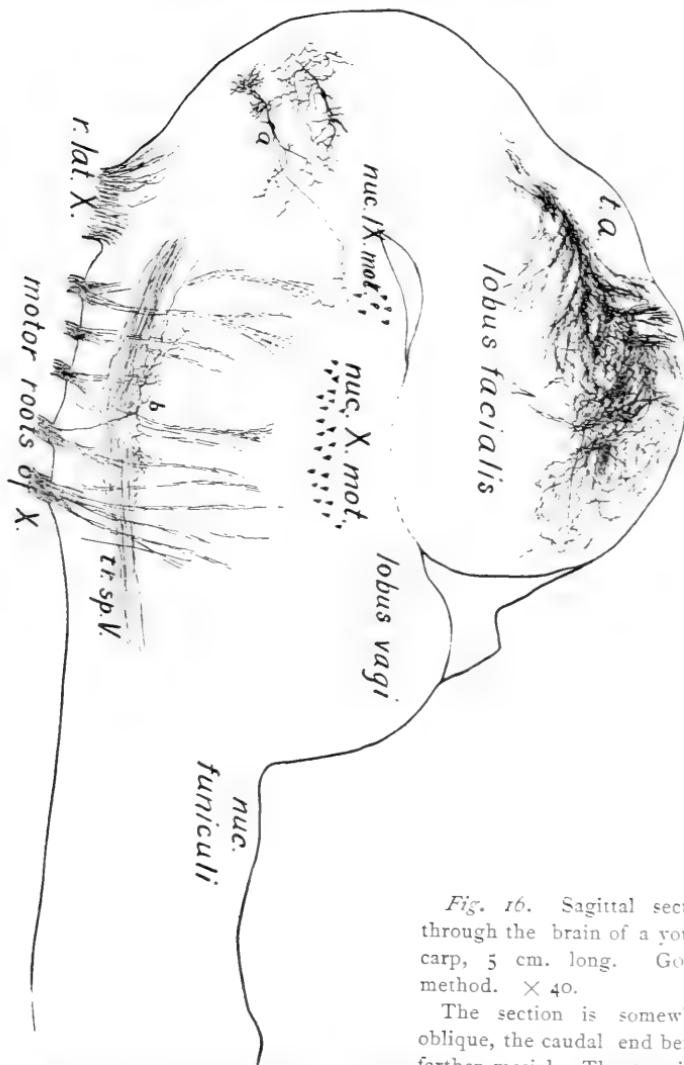
Fig. 16. Sagittal section through the brain of a young carp, 5 cm. long. GOLGI method. × 40.

The section is somewhat oblique, the caudal end being farther mesial. The terminal arborizations of the gustatory root of the facial nerve are richly impregnated. Two neurones are shown in the extreme cephalic part of the lobus IX, one of whose neurites (*a*) arborizes in the motor IX nucleus. These neurones lie in about the transverse level indicated in Fig. 17 and at the level of *r.IX.sen.* in Fig. 18. Their dendrites are reached by gustatory root fibers of the IX nerve. The neurone marked *b* is evidently of the same type as the one similarly designated in Fig. 18. *r.lat.X.*, ramus lateralis vagi; *t.a.*, caudal tip of tuberculum acusticum; *tr.sp.V.*, spinal V root.

Before proceeding with the description of the long second-ary gustatory tracts from the vagal lobe we shall describe the internal structures of the glossopharyngeal and facial lobes, as the long tracts from all these centers can best be described together.

Between the vagal and the facial lobes of cyprinoids is a small tuberosity which, as pointed out by B. HALLER ('96, p. 93 and Fig. 12), receives the glossopharyngeus nerve. It may be termed the *lobus glossopharyngei*. It is very distinct in forms like the gold-fish, Carassius, whose glossopharyngeus nerves are far separated from the vagus, the sensory IX nerve entering its dorsal side and the motor IX its ventral. It appears in the carp at a level somewhat cephalad of that shown in Fig. 5 along the line of union of the vagal and facial lobes. In this type it appears to receive from behind some fibers from the vagus roots; at any rate the IX and X roots are somewhat confused in this region. In both the carp and the gold-fish it receives from in front filaments of the communis root of the facialis. These filaments are very clearly shown arching over the dorsal side of the lobus IX in an oblique GOLGI section (Fig. 15, *a*); a certain part of the facial root apparently also reaches the cephalic end of the lobus vagi. It would be interesting to learn whether these facial fibers which separate from the facial lobe to end in connection with gustatory fibers from the mouth cavity coming in by the IX and X nerves are derived from the palatine and other facial branches which also supply taste buds within the mouth.

The lobus glossopharyngei has essentially the same connections as the lobus vagi. Fig. 16 gives an impregnation of two of the intrinsic neurones of the extreme cephalic part of the lobus IX in sagittal section of the brain of a young carp. The sensory (gustatory) fibers of the IX nerve end among the dendrites of these neurones. The neurone at the extreme left does not show its neurite, but the neurite of the one marked *a* is shown completely, arborizing in the motor IX nucleus, thus completing the simplest gustatory reflex arc for the IX nerve.

The structure of the *facial lobe* (tuberculum impar, ''lobus

trigemini," MAYSER) of the carp is considerably simpler than that of the vagal lobes. It is in general similar in internal organization to the facial lobes of Ameiurus, though its cells are of quite different form and it differs externally in that there is a complete fusion in the middle line of the right and left lobes with no clearly defined external or internal boundary between them.

Fig. 17. Transverse section through the facial lobe of *Minytrema melanops* (Raf.). GOLGI method. × 40.
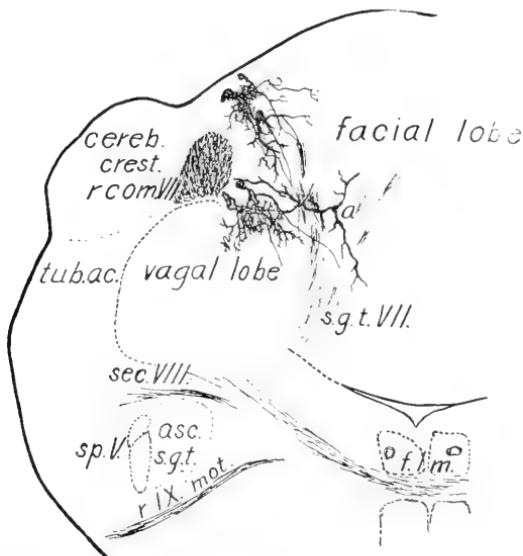
The section passes through the cephalic part of the facial lobe and includes the extreme cephalic end of the vagal lobe and the caudal end of the tuberculum acusticum. It shows five chief secondary gustatory neurones at the surface of the lobe and internally at *a* an imperfect impregnation of a cell of the intermediate zone of the same type shown in Fig. 18, *a*.

asc.s.g.t., main ascending secondary gustatory tract; *f.l.m.*, fasciculus longitudinalis medialis; *r.com. VII*, communis (gustatory) root of the facialis; *r.IX. mot.*, motor root of the glossopharyngeus; *sec. VIII*, secondary fibers from the tuberculum acusticum to ventral commissure; *s.g.t. VII*, secondary gustatory tract from the facial lobe; *sp. V*, spinal V tract; *tub.ac.*, tuberculum acusticum.

The center of the lobe is filled with very small intrinsic neurones arranged in dense clusters or rosettes of from 10 to 100 cells each. In Fig. 5 the clear spaces in the neuropil of the
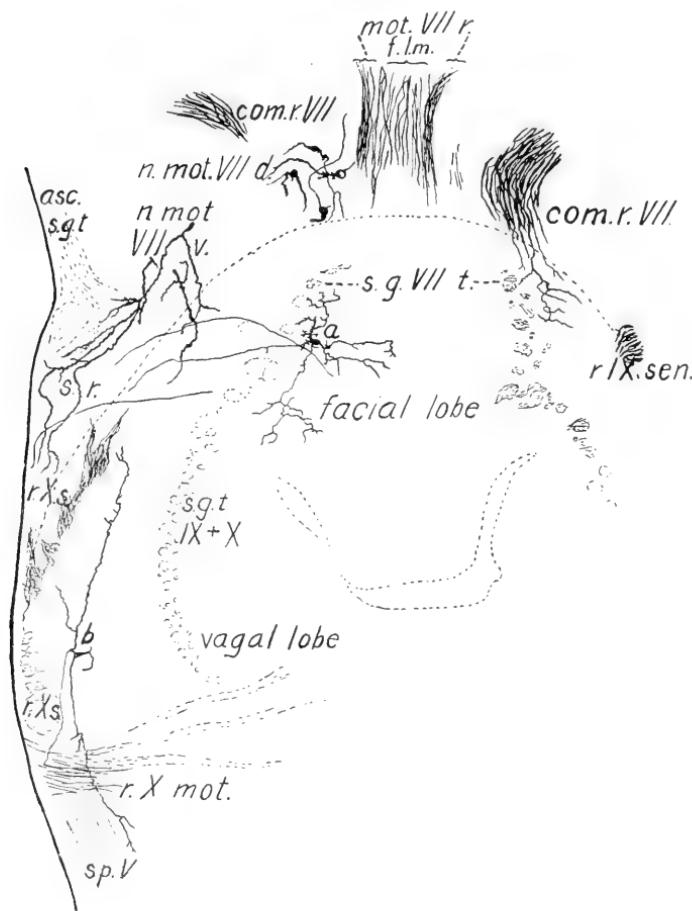
Fig. 18. Horizontal section through the base of the vagal and facial lobes of *Minytrema melanops* (Raf.). GOLGI method. × 40.

The section is slightly oblique, the left side being farther ventral. It passes through the ventral part of the facial and vagal lobes, illustrating a neurone (*a*) of the intermediate zone of the facial lobe. The dendrites spread throughout the lateral part of the lobe and the neurite passes laterally to enter the substantia reticularis of the oblongata (*s.r.*), here coming into relation with dendrites of the motor VII nucleus, as shown in the figure, and with other motor nuclei. The section shows the position of the dorsal tip of the motor VII nucleus (*n.mot. VII.d.*) and the motor VII root springing from it. The motor VII dendrites which are shown ramifying in the substantia reticularis (*n.mot. VII.v.*) spring from cells of the motor VII nucleus lying ventrally and laterally of those figured and out of the plane of this section. The neurone *b* is drawn in from the section lying next ventrad in the same series.

facial lobe represent the positions of some of the larger of these rosettes. Superficially there is a layer of chief gustatory neurones of the same general form as those of the vagal lobe (Fig. 17), whose neurite springs from the tip of a dendrite and passes at once into the secondary gustatory tract. The peripheral gustatory neurones enter by the communis root of the facial nerve (= dorsal geniculate root of the trigeminus, MAYSER = portio intermedia of WRISBERG in human anatomy) and pass back to the lobe as a huge tract of heavily medullated fibers close to the median line, constituting the pre-vagal portion of the fasciculus communis of OSBORN (= fasciculus solitarius of mammals). Entering the lateral border of the facial lobe, it spreads out in many strands in the superficial layer among the dendrites of the chief gustatory cells (cf. Figs. 5, 16 and 20). These endings are thick, loosely branched arborizations of wide extent. One of the simpler forms of these endings is impregnated in Fig. 18 on the right side.

There is no well defined motor layer of the facial lobe corresponding with that of the vagal lobe, but the ventro-lateral portion along the line of attachment to the oblongata is of different structure from the rest and will be termed the intermediate zone, or *nucleus intermedius facialis.* It contains rather large neurones whose dendrites spread widely through the whole lateral part of the facial lobe and whose neurites reach the substantia reticularis (Figs. 18, *a* and 17, *a* and 8). Here they reach directly the dendrites of the motor VII and less immediately those of the motor V, IX and X nuclei. This is the main pathway for short reflexes from the facial lobe to the oblongata. The absence of a motor layer in the facial lobe which gives rise directly to motor root fibers, like that in the vagal lobe, is to

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a, neurone of the intermediate zone; *asc.s.g.t.*, main ascending secondary gustatory tract; *com.r. VII*, communis (gustatory) root of the facialis; *f.l.m.*, fasciculus longitudinalis medialis; *n.mot. VII.d.*, dorsal part of motor VII nucleus; *n.mot. VII.v.*, ventral part of motor VII nucleus; *mot. VII.r.*, motor root of facial nerve; *r.IX.sen.*, sensory root of the IX nerve; *r.X.mot.*, motor root of the vagus; *r.X.s.*, gustatory root of the vagus; *s.g.t.IX+X*, secondary gustatory tract from X and IX lobes; *s.g. VII.t.*, secondary gustatory tract from the facial lobe; *s.r.*, substantia reticularis; *sp. V*, spinal V tract.

be correlated with the fact that its gustatory impressions come mainly from the outer skin and so give rise to more general body movements, such as turning and seizing, rather than to movements of the intrinsic musculature of the palatal organ, for which the root fibers of the motor layer of the vagal lobe are mainly designed. The substantia reticularis is known to be related not only to the cranial motor nuclei of the branchial or visceral type, as mentioned above, but also to contain cells whose neurites reach the fasciculus longitudinalis medialis and other paths with somatic motor connections (see CAJAL, '96, p. 129 and Fig. 16), so that we have here a very direct mechanism for producing the movement of eye-muscles and trunk-muscles necessary for locating and approaching a sapid substance which has been perceived by contact with taste buds of the outer skin.

2. *Secondary Gustatory Tracts.*

The secondary connections of the vagal, glossopharyngeal and facial lobes are of two general types :—(1) short paths, by way of the intrinsic secondary neurones or of collaterals of the neurites of the chief cells, directly to the motor layer of the vagal lobe and to the substantia reticularis of the oblongata ; and (2) long paths to regions above and below the oblongata, arising from the chief gustatory neurones. The connections of the first type are diffuse and largely unmedullated ; they have been briefly described above. The connections of the second type are compact well defined tracts of medullated fibers which will be termed the ascending and descending secondary gustatory tracts.

A word of further explanation may be necessary here in justification of the term *gustatory* as applied to these tracts. We have seen above that the communis roots of the VII, IX and X nerves in fishes generally contain fibers from taste buds in the mucous membrane of the mouth or in the outer skin and also fibers which end peripherally by free arborizations unrelated to any specialized sense organs—undifferentiated visceral endings. In view of the fact that these types of fibers, so distinct peri-

pherally, have not as yet been clearly separated at their central terminations, these roots must for the present retain the name "communis system," pending the time when they can be separated into specialized (gustatory) and unspecialized visceral components. With the secondary pathways and centers, however, the first step in this analysis may already be taken, thanks to the advantages of the comparative method.

In forms like the mammals, where the gustatory system is reduced, the analysis of these two elements in the fasciculus solitarius and its associated grey and secondary tracts will probably be impossible save by a degeneration method. The same applies to the amphibia, where the term fasciculus communis was first applied to the homologous structure. In fishes, again, we have some forms with reduced organs of taste, where the problem offers the same difficulties as in the cases cited, and also forms with enormous hypertrophy of the peripheral gustatory system with no appreciable change in the unspecialized component. In the latter cases whatever enlargement of the primary and secondary centers has taken place may clearly be assigned to the gustatory and not to the general visceral system. This is the case presented by the cyprinoid and siluroid fishes particularly, where the whole of the facial lobe and its connections and the greater part of the vagal lobe and connections have clearly arisen in response to the demands of the enormous peripheral gustatory system. While the diffuse connection of these centers with the substantia reticularis is known to have a parallel in the similar connections of the fasciculus solitarius of mammals and therefore doubtless in part pertains to the unspecialized visceral component, the long secondary paths which we here term the secondary gustatory tracts are highly developed only in those fishes possessing elaborate peripheral gustatory systems. This seems to constitute sufficiently good evidence that these long paths are mainly and perhaps wholly gustatory in function.

The neurites of the chief secondary gustatory neurones of the vagal and facial lobes, as we have seen, pass out in thick bundles to the ventro-lateral border of the oblongata, where they

turn to take a longitudinal course parallel with and often almost completely enclosing the spinal V tract. This secondary tract is largely composed of small and feebly medullated fibers, so that in WEIGERT sections it appears paler than the spinal V and the other great longitudinal conduction paths of the oblongata. Part of its fibers turn caudad and part cephalad. We therefore have descending and ascending secondary gustatory tracts (tractus gustus secundus descendens et ascendens) from both the vagal and facial lobes.

(1) Descending Secondary Gustatory Tract.

In the carp, as shown by WEIGERT sections of the adult, the descending tracts from both the vagal and facial lobes are very extensive. From the facial lobe they constitute a massive aggregate of medullated fibers in the "secondary vagus bundle" complex. But the descending tracts from the vagal lobe are largely unmedullated fibers scattered through the substantia reticularis grisea of the oblongata.

The descending secondary facial tract arises, as in Ameiurus, chiefly from the cephalic portion of the lobus facialis. The fibers pass ventro-lateral to gather in a compact bundle mesially and dorsally of the spinal V tract, farther caudad enclosing this tract on all but its external aspect (Fig. 5, *d.s. VII*). There is no obvious addition of descending fibers to this descending bundle in the region of the lobus vagi. It can be easily distinguished from the ascending secondary gustatory tract from the vagal lobe (Fig. 5, *a.s. X*) by the fact that the latter tract is much more feebly medullated at this level.

In the caudal part of the vagal lobe the motor zone is greatly thickened as is also the substantia reticularis grisea, which lies ventro-laterally of it and in intimate relations with the layer of secondary gustatory tracts of the vagal lobe, the descending secondary facial tract and the spinal V tract. This whole area contains descending secondary vagal fibers. These are chiefly very fine unmedullated or feebly medullated fibers passing from the layer of secondary gustatory tracts of the vagal lobe caudad and mesad through the substantia reticularis grisea
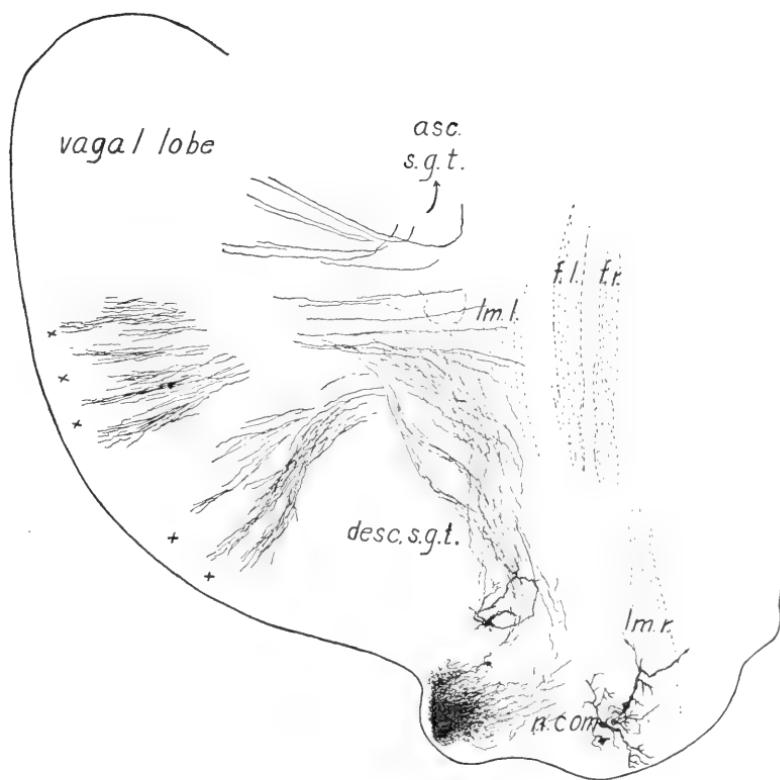
Fig. *19.* Longitudinal section through the left vagal lobe of a young carp, 5 cm. long. GOLGI method. × 40.

The section is approximately horizontal, but strongly inclined so that the left side is farther dorsal. It shows the descending secondary gustatory tract (*desc. s.g.t.*) from the vagal lobe to the region of the nucleus funiculi. At the periphery of the vagal lobe in the regions marked by the crosses there is a very rich impregnation of cells among which the secondary fibers arise, which are omitted so as not to confuse the drawing, since they are too densely impregnated to permit an accurate determination of their relations to the fibers. These cells are partly chief secondary neurones like those of Fig. 7, and partly the smaller type as shown in Fig. 11. A very few fibers of the ascending secondary gustatory tract (*asc.s.g.t.*) from the vagal lobe are shown. This tract appears voluminously a few sections ventrad in the position indicated by the arrow. The median line is indicated by the position of the left and right fasciculi longitudinales mediales (*f.l.* and *f.r.*). The lemniscus on both the left (*lm.l.*) and right (*lm.r.*) sides is shown; also the position of the funicular nucleus and commissural nucleus of CAJAL (*n.com.*).

in diffuse formation to reach the region of the nucleus funiculi and commissura infima HALLERI (Figs. 19, 11). The indications are that it springs mainly from the smaller secondary neurones of the lobe (cf. Fig. 11), though I have no conclusive evidence that the chief secondary cells do not also participate in its formation.

In the region of the funicular nuclei the substantia reticularis grisea, related above with the vagal lobe, enlarges. This I term the *inferior secondary gustatory nucleus* (nucleus gustus secundus inferior). It receives the diffuse tracts from the vagal lobe just described, and also the greater part of the descending secondary facialis tract. A portion of the latter tract, however, continues into the spinal cord caudad of the funicular nuclei in the ventro-lateral tracts.

This inferior gustatory nucleus is intimately related with the termini of the spinal V tract, funicular nuclei, commissura infima HALLERI and commissural nucleus of CAJAL. It is clearly a coordination center between gustatory and tactile sensory impressions. In fishes with feebly developed gustatory system it is of insignificant size. Its great development in the cyprinoids and, as we shall see, in the siluroids is correlated with the known feeding habits of these fishes. It has been shown (JUDSON HERRICK, '04) that fishes with taste buds in the outer skin taste with these organs and habitually localize the food stimulus partly by the sense of taste and partly by tactile stimulation of the same cutaneous areas. It may safely be inferred that the descending secondary gustatory connections of these fishes are especially adapted to serve this correlation of the senses of taste and touch as employed in localizing peripheral stimuli in the search for food and to call forth the bodily movements necessary to seize the food when its position has been determined.

The detailed description of these connections involves the discussion also of the secondary connections of the general cutaneous (somatic sensory) system of neurones and must be reserved for a later contribution.

(2)   Ascending Secondary Gustatory Tract.

This tract, which takes the greater part of the fibers aris-

ing from the chief secondary gustatory neurones of both the vagal and facial lobes, is one of the most distinctive features of the teleostean brain. In the two groups here treated, particularly, it attains enormous dimensions, constituting the "Sekundäre Vagus-Trigeminusbahn" of MAYSER, whose excellent description ('82, p. 318) is fully confirmed. It is included in the "system γ" of the descriptions of GORONOWITSCH ('88, and '96). The curious notion of B. HALLER ('96, p. 92) that this is a descending tract from the cerebellum and other higher cerebral regions to the sensory centers in the vagal lobe need not detain us, for he gives no evidence for such a view. The common designation of this tract as "secondary vagus bundle" is inadmissible, since in all fishes it contains secondary glossopharyngeus and facialis fibers also, the secondary facialis fibers preponderating in siluroids. Moreover, there are other secondary vagus tracts for general cutaneous and other types of fibers, besides the descending and short gustatory paths described in the preceding section.

The ascending or central gustatory tract takes its position ventrally and mesially of the spinal V and descending secondary facialis tracts and partly enclosing them (Fig. 5, *a.s.X.*). It ascends to the level of the superficial origin of the sensory trigeminus root from the oblongata, where it turns mesially and dorsally to enter its own terminal nucleus (superior secondary gustatory nucleus, Fig. 20). The axial portion of this nucleus was termed by MAYSER "Rindenknoten" and by JOHNSTON ('01) secondary vagus nucleus. It is included in the "Uebergangsganglion" of MAYSER's descriptions, this latter group of cells being very complex and not as yet fully understood. Its homologies are considered in the final section of this paper.

It lies in the dorsal part of the isthmus ventrally of the line of fusion of the valvula cerebelli with the body of the cerebellum. Typically it lies near the median line and projects into the aquaeductus, but in some cyprinoids it is so greatly enlarged as to reach also to the lateral surface of the brain at the isthmus and there project as a distinct tuberosity between the caudal end of the tectum opticum and the tuberculum acusticum

(Fig. 3, lower figure). It lies cephalad, dorsad and mesad of the motor V nucleus, the long dendrites of some of whose cells pierce it and come into relations with some of the termini of the gustatory fibers (Figs. 21 and 23). The motor V nucleus is very large in these fishes and extends far cephalad and dorsad in intimate relations with the termini of the secondary gustatory tract. The dendrites of these motor cells spread out widely in every direction and are not directed ventro-laterad so generally as in the case of the motor nuclei of the VII, IX and X nerves. In fact, the greater part of them take the opposite course, as figured, into the caudal part of the secondary gustatory nucleus and the adjacent substantia reticularis grisea.

This fact, together with others of similar import, suggests the morphological interpretation of this secondary terminal nucleus; viz., that it is merely a specialization from the substantia reticularis. CAJAL ('96, p. 128) has confirmed the view

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Fig. 20. Parasagittal section through the brain of the spotted sucker, *Minytrema melanops* (Raf.). GOLGI method. × 12.

The sketch is designed to illustrate the course of the ascending secondary gustatory tract and the connections of its terminal nucleus. The plane of the section is slightly oblique so that the caudal end and the ventral side are nearer the median line than are the cephalic and dorsal borders. The figure is a composite, made by outlining one section with the camera lucida and filling in the details from this section and the three sections of the same series on each side immediately adjacent, omitting irrelevant detail. The features introduced are schematized as little as possible. The whole course of the ascending secondary gustatory tract from the facial lobe is shown. The origin of the tract from the vagal lobe lies farther lateral.

b., tract between secondary gustatory nucleus and n. lateralis valvulae ; *com.h.*, commissura horizontalis, FRITSCH ; *com.r. VII*, communis (gustatory) root of the facialis; *desc.sec. X*, descending secondary gustatory tract from the vagal lobe ; *f.l.m.*, fasciculus longitudinalis medialis ; *inf.lob.lat.*, lateral lobule of inferior lobe (hypoaria, C. L. HERRICK) ; *inf.lob.m.*, median lobule of inferior lobe (mammillare, C. L. HERRICK) ; *n.cort.*, nucleus corticalis, FRITSCH ; *n.IX*, motor nucleus of the glossopharyngeus ; *n.lat.*, nucleus lateralis valvulae ; *n.rot.*, nucleus rotundus, FRITSCH ; *n.st.*, nucleus subthalamicus, C. L. HERRICK ; *n. V.*, motor nucleus of the trigeminus ; *n. VII*, motor nucleus of the facialis ; *r.X.s.*, sensory root fibers of the vagus ; *sec.gust.t.*, ascending secondary gustatory tract from the facial and vagal lobes ; *tr.l.b.*, tractus lobo-bulbaris ; *tr.t-c.*, tractus tecto-cerebellaris ; *tr.t.lob.*, tractus tecto-lobaris, JOHNSTON (commissura ventralis, C. L. HERRICK). The area marked *n.funiculi* contains also the inferior secondary gustatory nucleus.
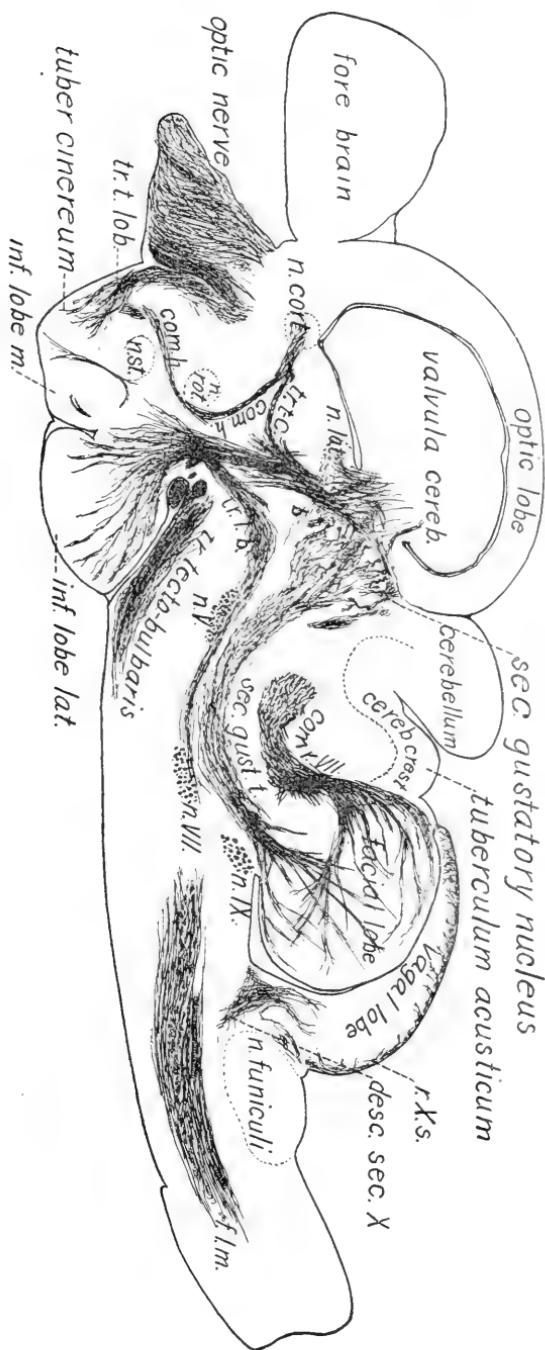
of KÖLLIKER that the substantia reticularis alba is composed of sensory bundles of the second order and that the substantia reticularis grisea is a sensory field of the third order, designed to distribute sensory excitations from the V, IX and X nerves (and also, it should be added, from the VII nerve) over a large
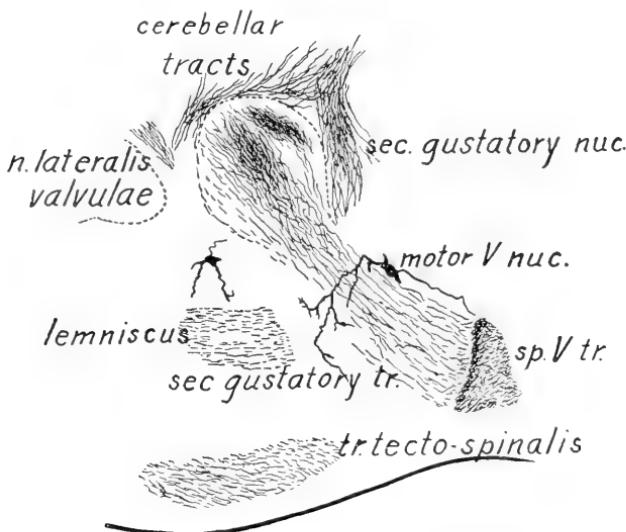
Fig. 21. Portion of a sagittal section of the brain of *Minytrema melanops* (Raf.). GOLGI method. × 40.

The section is quite oblique, the cephalic end and the dorsal side being inclined toward the median line. It passes through the ascending secondary gustatory tract at the point where it enters its terminal nucleus under the cerebellum (the cephalic end of the figure being at the left). The spinal V tract (*sp. V.tr.*) is cut close to its superficial origin from the periphery. A single neurone of the most dorsal part of the motor V nucleus is impregnated, one of its dendrites crossing the mesial side of the gustatory tract to ramify in the most ventral and caudal part of the layer of chief tertiary gustatory neurones, a single one of which is impregnated. The tertiary gustatory path does not lie in the plane of this section (cf. Fig. 23).

field of motor nuclei of the oblongata. This definition, it will be observed, carries also the secondary gustatory nucleus, save that in addition to direct relations of the secondary termini with the motor nuclei, like the trigeminal connection just described, there is here, as we shall see, a much more extensive development of tertiary neurones for connections of a higher order in

the floor of the thalamus (central tertiary tract). The dorsal
and mesial position of this derivative of the substantia reticular-
is is easily explained by the topographic features of the isth-
mus. Here the ventro-lateral region is occupied by the great
conduction paths between the oblongata and the mid-brain—
the tractus tecto-spinalis, tractus lobo-spinalis, lemniscus, etc.
The dorso-lateral region is occupied by the tuberculum acusti-
cum and its cerebellar connections. The enlarged secondary
gustatory terminal is prevented from growing caudad by the
great cerebellar crest and tuberculum acusticum. It must,
therefore, grow upward, inward and forward into the optocoele.
In this position it appears typically in all teleosts. But when
still more enlarged, as in cyprinoids, further growth in this
direction being prevented by the valvula cerebelli, which is also
very large in these fishes, it is forced to grow outward until it
appears as a superficial eminence cephalad of the tuberculum
acusticum and dorsally of the great ventro-lateral conduction
paths just referred to (Fig. 3).

The secondary gustatory nucleus does not, however, com-
prise the whole of the substantia reticularis grisea of this region
of the isthmus. For caudo-mesially of this nucleus at the level
where the secondary gustatory tract enters it from the lateral
side of the oblongata is another considerable cellular area which
represents a less highly specialized portion of the same sensory
field. This also borders the ventricle, in some types forming a
considerable projection into it from the lateral wall immediately
caudad and ventrad of the commissure of the secondary gusta-
tory nuclei. Its anomalous position is brought about by the
same forces which were discussed above in connection with the
secondary gustatory nucleus. It is in very intimate relation
with the motor V nucleus which lies ventro-laterally of it and it
apparently is the chief medium of communication between the
various sensory pathways and that nucleus. Its neurones, in
other words, are like the others of the substantia reticularis
grisea in being of the tertiary sensory type and discharging into
a motor field, in this case the V nerve. It may therefore be
termed the *substantia reticularis grisea trigemini.*

The position of this area of the carp is indicated in Fig. 22. It is reached, as shown in the figure, by a slender branched process of one of the chief tertiary neurones, which may be a dendrite, but more probably is a collateral neurite, though it does not spring from the main neurite (*n*), which enters the tertiary tract separately. The neurone marked *a* lies in the adjacent section and is drawn enlarged in Fig. 25. From the base
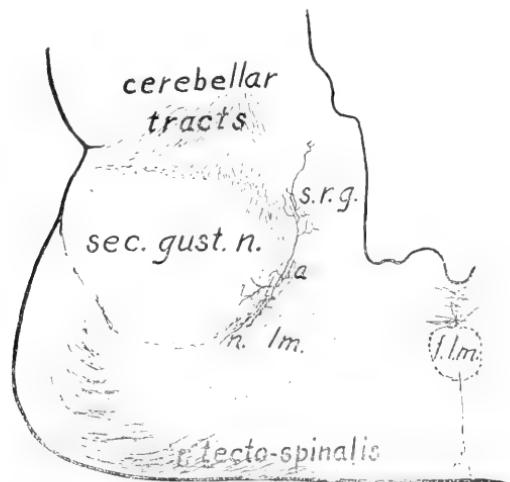
Fig. 22. Section taken through the superior secondary gustatory nucleus of the carp. GOLGI method. ×40.

The section is approximately transverse, but strongly inclined so that the dorsal and right sides are father caudad. A single chief tertiary gustatory neurone is shown, whose neurite (*n*) enters the tertiary gustatory tract. Its main dendrite passes out of the plane of the section (cf. Fig. 25). A much more slender process is completely impregnated, running dorsad and caudad to reach the substantia reticularis grisea trigemini (*s.r.g.*). At *a* is shown the position of the neurone drawn in Fig. 25, which lies in the section adjacent to the one here drawn. The secondary gustatory nucleus is bordered on the dorsal and mesial sides by the fibers of the tertiary tract.

of its neurite is given off a collateral, only a part of which is shown, which is probably of the same type as the one here figured. Contiguous sections of the same series show fibers passing from this area of substantia reticularis directly into the axis of the secondary gustatory nucleus and there arborizing, which probably represent dendrites of the cells of the substantia reticularis which are not impregnated.

These fragmentary data are sufficient to show that we have in addition to direct connections of dendrites of the motor V nucleus with secondary gustatory fibers, a similar but indirect functional connection via the substantia reticularis grisea trigemini. The numerous other connections of the latter area need not now concern us.

One of my GOLGI preparations of the carp shows dendrites of a very large neurone lying in the vicinity of the nucleus of origin of the IV nerve sending dendritic branches ventrad into the region caudad of the commissura ansulata and other large branches farther caudad and laterad into the same portion of the secondary gustatory nucleus which is reached by dendrites of the motor V nucleus. The impregnation is so imperfect that it is impossible to be sure whether this neurone belongs to the motor nuclei of the eye muscle nerves or to the fasciculus longitudinalis medialis or to some other neighboring structure.

3. Superior Secondary Nucleus and its Connections.

The superior secondary gustatory nucleus presents, broadly speaking, the same general arrangement as the primary end-station in the vagal and facial lobes. That is, the secondary neurones end in relation with two types of tertiary neurones (1) intrinsic neurones, filling the interior of the nucleus (''Rindenknoten,'' MAYSER) and (2) the chief tertiary neurones in a dense layer around the periphery. The chief difference between the arrangement of the primary and secondary end-stations lies in the fact that the latter is connected with its fellow of the opposite side by a broad commissure, the commissure of the secondary vagus nuclei of JOHNSTON. As was recognized by MAYSER, this commissure contains fibers of at least two sorts (1) neurites of the intrinsic tertiary neurones, (2) terminals of a portion of the secondary gustatory tract. From (2) it follows that the secondary tracts end partly on the same side and partly in the secondary nucleus of the opposite side, the former portion being much the larger. The uncrossed portion ends by free arborizations within the secondary nucleus and also extensively in the cortical

portion among the chief tertiary cells (Fig. 23). The details of the endings of the crossed fibers I have not been able to observe, but there is every reason to believe that they are essentially similar.

I have no complete impregnations of the intrinsic commissural neurones. The evidence is that their delicate, feebly medullated neurites gather in the interior of the nucleus and terminate after crossing among the dendrites of the chief tertiary neurones of the opposite side. The layer of these chief cells envelopes the secondary nucleus on all sides except where it is interrupted by the secondary and commissural tracts. The neurites of these cells pass directly outward and become medullated as they enter the chief tertiary tract for the inferior lobe. Just external to the layer of tertiary neurones the gustatory nucleus is encapsuled by a dense layer of heavily medullated nerve fibers. These are partly the tertiary fibers, but chiefly cerebellar tracts. The position of the secondary gustatory nucleus in the isthmus is such that the cerebellar penduncles, passing downward from the cerebellum and valvula, almost entirely envelop it. It is this peculiarity which suggested to MAYSER the name "Rindenknoten." Surrounding this fibrous capsule is an aggregate of nuclei with very diverse connections to which MAYSER applied STIEDA's name, "Uebergangsganglion."

This region is perhaps the most intricate and difficult of analysis in the teleostean brain, as it contains several large centers and numerous important tracts, both medullated and unmedullated, all crowded into a very small space. The dorsal part of the isthmus is more than usually crowded in these types, not only by these great gustatory centers, but also by the enlarged cerebellum and valvula and their associated tracts.

The broad line of fusion of the valvula cerebelli with the torus semicircularis (colliculus) is occupied by a very dense mass of cells and medullated and unmedullated tracts whose relations are only imperfectly shown in my preparations. The whole complex, which lies mesially of the nucleus lateralis mesencephali (EDINGER), or colliculus, I term provisionally the nucleus lateralis valvulae. It is, apparently, the most cephalic

part of the "Uebergangsganglion" of STIEDA. This group of cells fuses behind with the dorsal and cephalic border of the secondary gustatory nucleus, but is separated from it more or less definitely by the medullated vertical cerebellar tracts which encapsule the secondary gustatory nucleus. Sections stained by the method of PAL show large tracts of fine fibers with ex-
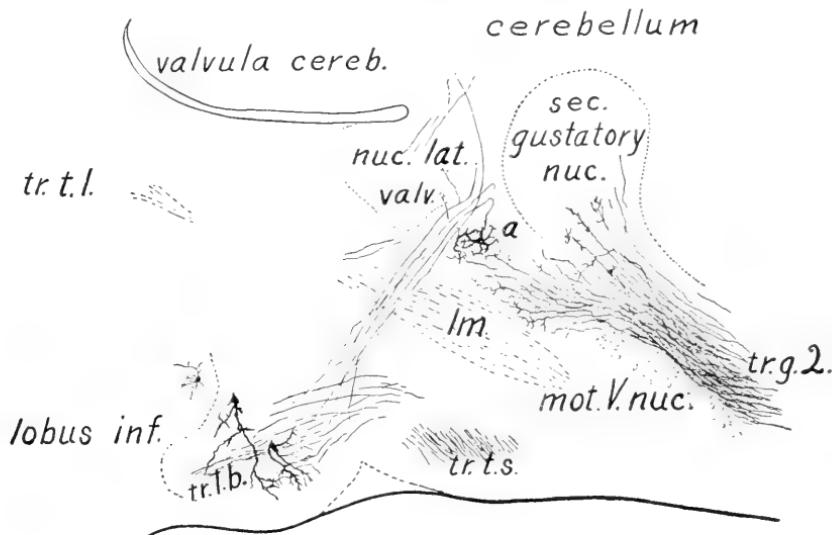
Fig. 23. Portion of sagittal section of the brain of a young carp, 5 cm. long. GOLGI method. × 40.

The ventral side of the preparation is below and the cephalic end at the left. The section includes the superior secondary gustatory nucleus ("Rindenknoten," MAYSER) and shows the origin and course of the tertiary path to the inferior lobe. A single neurone of the latter type is impregnated completely (*a*) save for the terminal arborization. Mingled with the neurites of these cells are those of the tract between the cerebellum and the inferior lobe (tractus lobo-cerebellaris, EDINGER). Among the terminals of the tertiary tract are the cells of origin of the tractus lobo-bulbaris et spinalis (*tr.l.b.*); *l.m.*, lemniscus ; *tr.t.l.*, tractus tecto-lobaris ; *tr.t.s.*, tractus tecto-spinalis.

ceedingly delicate medullary sheaths passing dorso-ventrally between the n. lateralis valvulae and the cerebellum and valvula (Fig. 24), and GOLGI sections show diffuse unmedullated tracts taking the same courses (Fig. 20). Whether the medullated and the unmedullated fibers spring from neurones of the same type, I have not been able to determine. The neurones shown
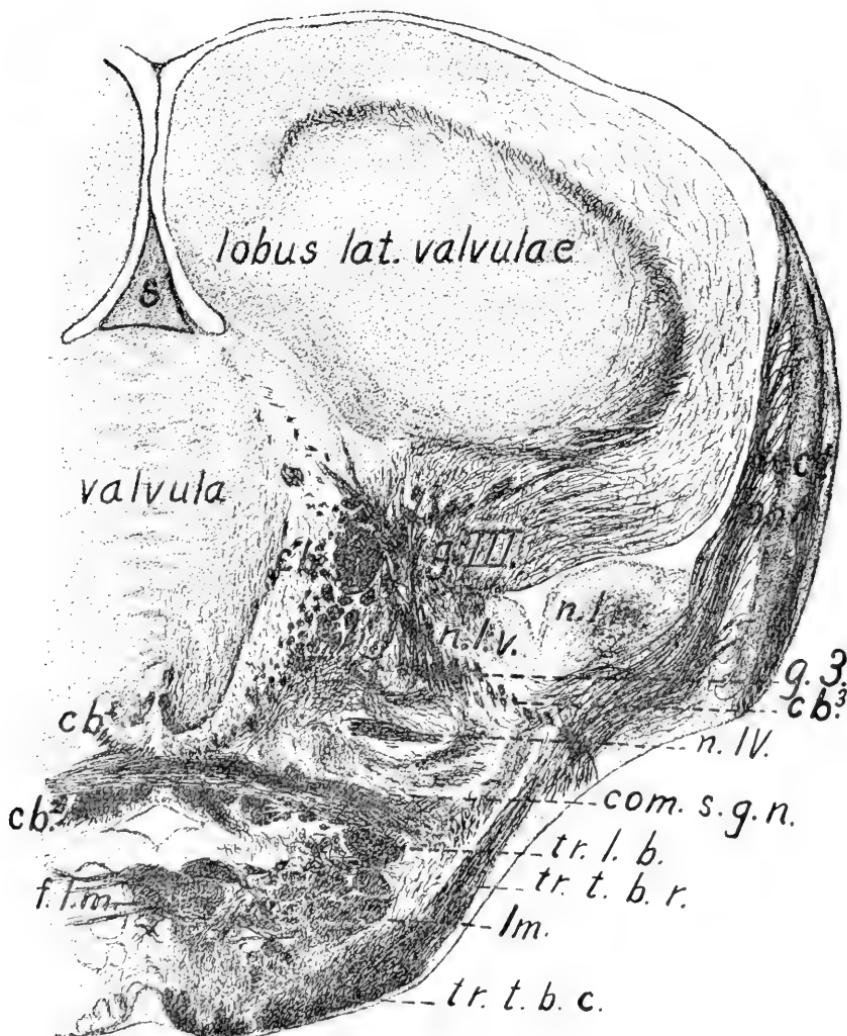
Fig. 24.   Transection through the brain of a large carp just cephalad of the superior secondary gustatory nucleus.   Stained by the method of WEIGERT-PAL. × 20.

   The section passes through the most cephalic portion of the commissure of the secondary gustatory nuclei, and illustrates the relations of the nucleus lateralis valvulae to this nucleus and to the cerebellum.   The trochlearis (*n.IV.*) decussates just cephalad of the gustatory commissure and in passing to its super-

by the GOLGI sections are like the cells of the granular layer of
the cerebellum and probably are of that type, receiving afferent
cerebellar impulses and transmitting them to the cortex cerebelli.
Whether they receive their impulses from the adjacent gusta-
tory nucleus or from other sources, my preparations do not
show with certainty, but probably partly from the former.

There is also a broad unmedullated connection between
the ventral part of the secondary gustatory nucleus and the
cephalic part of the n. lateralis valvulae, running cephalad
through the vertical cerebellar tracts (designated by *b* in Fig.
20). Horizontal sections of the brain of Catastomus show nu-
merous delicately medullated fibers running between the whole
cephalic face of the gustatory nucleus and the n. lateralis valvu-
lae. These connections lend further support to the belief that
the n. lateralis valvulae is in part a gustatory intermediary sta-
tion for the cerebellum. This nucleus extends cephalad to the
point where the valvula severs connection with the floor of the
mesencephalon and here a large tract passes between its cephal-
ic end and the nuclei of the third nerve and of the fasciculus
longitudinalis which lie mesially of it. It is no doubt this con-
nection which led B. HALLER to state ('98, p. 522) that the
"Uebergangsganglion of FRITSCH and MAYSER is an "upper
motor oculomotorius nucleus." The nucleus lateralis valvulae

ficial origin become embedded in the most cephalic part of the secondary gusta-
tory nucleus, the latter being represented in the figure by the neuropil surround-
ing *n.IV.* Sections immediately caudad show the gustatory nucleus occupying
the entire space from near the median line to the lateral surface of the brain and
from the level of the commissural fibers and tr. lobo-bulbaris (*tr.l.b.*) up to the
valvula cerebelli.

cb., *cb*¹., *cb*²., *cb*¹., cerebellar tracts ; *com.s.g.n.*, commissure of the secondary
gustatory nuclei ; *f.l.m.*, fasciculus longitudinalis medialis ; *g.III*, fibers arising
from the granule cells of the nucleus lateralis valvulae and passing dorsally into
the lateral lobe of the valvula cerebelli ; *g.3.*, tertiary gustatory tract for the
inferior lobe appearing as oval bundles among the strands of the cerebellar tract
*cb*³.; *lm.*, lemniscus (fasciculus lateralis); *n.IV.*, root of the fourth nerve ; *n.l.m.*,
the extreme caudal end of the nucleus lateralis mesencephali (torus semicircularis,
colliculus); *n.l.v.*, nucleus lateralis valvulae ; *s.*, a large blood sinus between the
lateral lobes of the valvula ; *tert.opt.*, tectum opticum ; *tr.l.b.*, tractus lobo-bulbar-
is ; *tr.t.b.c.*, tractus tecto-bulbaris et spinalis cruciatus ; *tr.t.b.r.*, tractus tecto-bul-
baris et spinalis rectus.

has other connections (with the substantia reticularis of the oblongata, optic thalamus, etc.) which I have not yet fully worked out. Its homologies are discussed briefly beyond. Another part of the "Uebergangsganglion" which serves as a gustatory reflex center is the nucleus already designated as substantia reticularis grisea trigemini. There remain several considerable collections of cells in the "Uebergangsganglion" which may have gustatory functions, but their discussion would involve a more extensive analysis of the mesencephalon than we can here attempt.

A typical illustration of the chief tertiary gustatory neurones in the cortex of the secondary gustatory center of the carp is seen in Fig. 25. The dendrite plunges into the axial portion of the nucleus ("Rindenknoton," MAYSER) and there spreads out widely among the termini of the secondary gustatory fibers (cf. Figs 22, 23). The neurite passes downward to enter at once the tertiary gustatory tract for the inferior lobe of the same side, where it takes up a dense medullary sheath and so is rarely completely impregnated in GOLGI preparations. These medullated fibers mingle immediately with similar ones of the cerebellar tracts (lobo-cerebellaris and others) which encapsule the secondary nucleus and which likewise pass into the inferior lobe, so that I have found it impossible in WEIGERT sections to effect the separation of the two classes of fibers except at the origin of the tertiary gustatory tract from its nucleus. I have, fortunately, secured a sufficient number of complete GOLGI impregnations to show the origin of the tract without uncertainty. Its entire extent save the terminal arborization is shown in Fig. 23.

The combined tract passes ventrad and somewhat cephalad to enter the caudal border of the inferior lobe and spread throughout the whole of the lateral lobule of this organ. Whether any of these fibers reach the median lobule my preparations do not definitely determine, but apparently not. (The terms lateral and median lobules are used in the sense defined by DAVID ('92). The lateral lobules are the hypoaria and the median lobules the mammillary bodies of C. L. HERRICK ('92)).

The terminal arborizations of this tract in the inferior lobe of Ameiurus shown in Fig. 37 probably belong to the gustatory component.

The *tractus lobo-bulbaris* arises from the whole of the lateral lobule of the inferior lobe and its fibers mingle with those of the tertiary gustatory tract, the two tracts, however, being well separated where they leave the lobe (Fig. 20, 23). The tractus lobo-bulbaris is the main path for descending impulses from the inferior lobe (gustatory and other reflexes) and was termed in MAYSER'S descriptions ('82, p. 319) ·'Nervenfaserbahn *x.*''
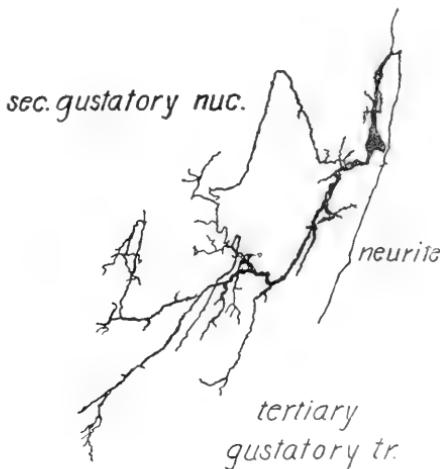
Fig. *25.* One of the chief tertiary neurones of the superior secondary gustatory nucleus of a young carp. GOLGI method. × 187.

For the relations of this neurone to the surrounding structures, cf. Fig. 22, which is drawn from the section next caudad. The dendrites spread out in the mesial part of the secondary gustatory nucleus. The neurite at once enters the tertiary gustatory tract for the inferior lobe and either passes out of the plane of the section or becomes medullated and so fails to impregnate.

The fact that it is larger (as mentioned by MAYSER) in cyprinoids and the peculiarities of its course in the oblongata make it probable that it is the chief motor return path for the higher gustatory reflexes. This of course is not its only function, for it clearly serves as the chief path for all descending impulses from the inferior lobe to the oblongata and cord, and therefore carries olfactory and other reflex impulses in addition to gustatory.

The course of the tractus lobo-bulbaris as it leaves the inferior lobe is clearly shown in some of my GOLGI preparations. In WEIGERT sections this tract is so confused at its origin with the fibers of the tractus lobo-cerebellaris and tertiary gustatory path that it cannot be clearly distinguished at first. Its fibers throughout their course are very fine and feebly medullated. The tract passes up from the inferior lobe and arches around the ansulate commissure to turn caudad along the inner border of the lemniscus. Upon reaching the level of the secondary gustatory nucleus it turns laterad over the dorsal surface of the lemniscus (Fig. 24) and takes up a position ventrally of the secondary gustatory nucleus (Fig. 20, *tr.l.b.*). Farther back it becomes partially enveloped by the ascending fibers of the secondary gustatory tract. The latter tract in cross section is crescent-shaped and the concavity of the crescent, which faces inward, is occupied by the descending fibers of the tractus lobo-bulbaris. This tract is thus placed along the dorso-lateral border of the substantia reticularis, which, as we have seen, is the chief avenue of communication with the motor nuclei of the oblongata. The tractus lobo-bulbaris diminishes caudad, breaking up in the substantia reticularis and so puts the gustatory center in the inferior lobe into relation with the peripheral musculature. It doubtless extends into the spinal cord, but it is impossible to distinguish its fibers from the others in the substantia reticularis alba farther back than the vagal lobes.

SECTION IV. THE CENTRAL GUSTATORY SYSTEM OF SILUROID FISHES.

As we have seen above, the anatomy and physiology of the peripheral gustatory system of the cat fishes, or horned pouts, is now well known. The cutaneous portion of the system is here hypertrophied, while the buccal portion is about as in other fishes. This is the explanation of the fact that the cat fishes possess enlarged facial lobes, while the vagal lobes are of the typical teleostean form. We shall now proceed to a description of the internal anatomy and secondary connections of these structures in Ameiurus and closely related species. The mater-

ial consists of serial sections of ten adult brains cut in the three
conventional planes and stained with DELAFIELD'S hæmatoxylin
and by the methods of WEIGERT and WEIGERT-PAL, together
with serial sections of about 100 younger brains prepared by
the method of GOLGI and cut in various planes.

The *vagal lobe* of the cat fish is essentially similar to that
of most other teleosts. The general relations as seen in tran-
sections stained by DELAFIELD'S hæmatoxylin are shown in
Fig. 26. The lobe is crowded with numerous small nerve cells,

dors. sec. neurones

intrinsic neurones

superfic. root of X

lat. sec. neurones

deep root of X

nuc. intermedius X
spinal V tract

desc. sec. VII tract

asc. sec. gust. tract

motor root of X

ventral cornu

n.amb.

s. r. g.

f.lm.
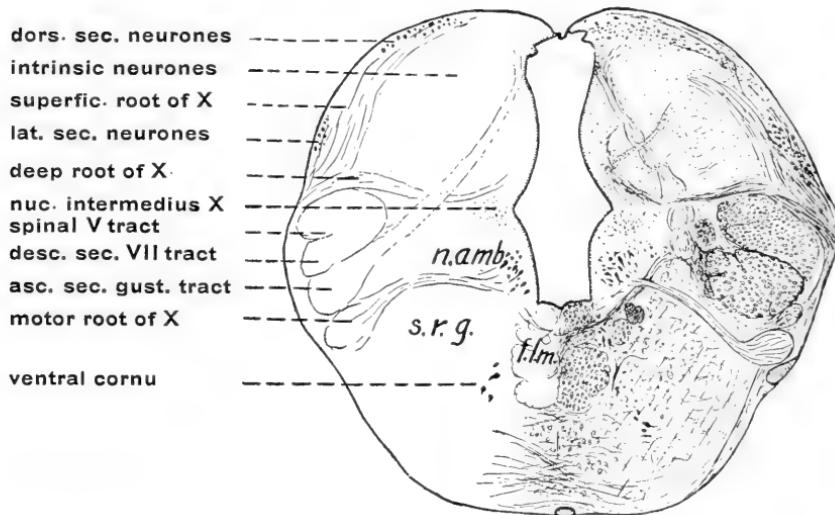
Fig. 26. Transverse section through the vagal lobes of a large adult of
Ictalurus punctatus (Raf.). Drawn from a hæmatoxylin preparation. ×16.

f.l.m., fasciculus longitudinalis medialis; *n.amb.*, nucleus ambiguus; *s.r.g.*,
substantia reticularis grisea.

which take up a very pale stain in hæmatoxylin. Most of
these intrinsic cells are neurones of GOLGI's type II, whose
processes do not extend beyond the lobe. Along the dorsal
and lateral borders of the lobe is a layer containing larger
cells whose nuclei stain very little in hæmatoxylin and whose
cytoplasm practically not at all. The axones of these cells con-
stitute the chief sensory conduction paths from the vagal lobe
to other parts of the brain, and I shall term them the dorsal

and lateral chief secondary gustatory neurones. Deeply embed-
ded in the substance of the medulla oblongata ventrally of the
main body of the vagal lobe is an area filled with cells some-
what larger than the intrinsic neurones but much smaller than
the chief secondary neurones, which may be termed intermedi-
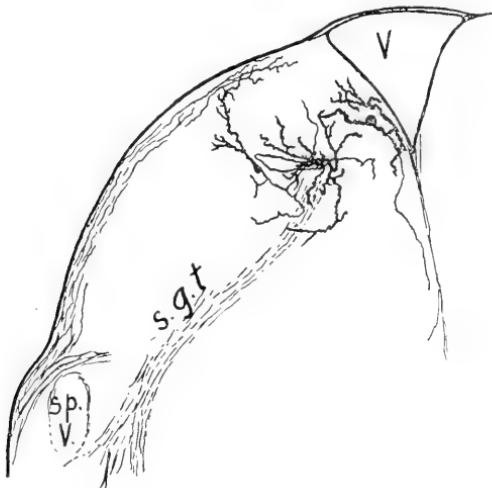
Fig. 27. Three intrinsic neurones of type II from the left vagal lobe of
Ameiurus nebulosus. From a GOLGI preparation. × 60.

The secondary communis tract(*s.g.t.*)which appears to arise among these cells,
in reality springs from cells lying farther dorsally which are not impregnated in
this preparation. Superficial root fibers of the vagus are impregnated at the bor-
der of the vagal lobe. *sp.V.*, spinal V tract; *V*, ventricle.

ary neurones (nucleus intermedius vagi). Their neurites enter
the substantia reticularis and other conduction pathways be-
tween the sensory and motor nuclei. Ventrally of the vagal lobe
and not properly to be considered a part of it is the nucleus
ambiguus, close to the median line in the floor of the fourth
ventricle. The communis roots of the IX and X nerves enter
the lobe at its ventro-lateral border, some descending along the
lateral aspect of the oblongata to the region of the commissura
infima HALLERI, forming the descending communis root of the
vagus, others passing directly inward under the lobe to termin-
ate in the lobe along its inner or ventricular border, forming the
deep communis roots of the vagus and glossopharyngeus, while

the main portion of the root fibers turn dorsally along the outer aspect of the vagal lobe to form the superficial communis roots of these nerves.

Communis root fibers, presumably bearing both general visceral and gustatory impulses, arborize freely in the entire inner, dorsal and lateral surfaces of the vagal lobe, some arbor-
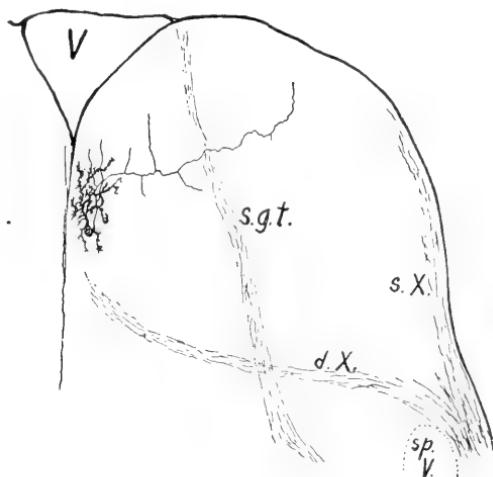
Fig. 28. An intrinsic neurone of the right vagal lobe of *Ameiurus nebulosus* seen in cross section. The cell body lies near the mesial border of the right vagal lobe and the neurite is directed laterally through the middle of the lobe. From a GOLGI preparation. ×60.

d.X., deep root of the vagus; *s.g.t.*, secondary gustatory tract; *sp. V.*, spinal V tract; *s.X.*, superficial sensory root of the vagus; *V*, ventricle.

izations also occurring in the center of the lobe. Impulses from the latter are taken up by the intrinsic cells and diffused throughout the entire lobe. For the forms of these cells see Figs. 27, 28, 29, 30, 34. It may be conjectured that these cells receive mainly the unspecialized visceral root fibers, since the gustatory fibers are here, as in cyprinoids, almost certainly related chiefly to the superficial groups of secondary neurones. Type II cells are abundant in elasmobranchs (HOUSER, '01), whose taste buds are few and confined to the mouth, but were not demonstratable in any of JOHNSTON's GOLGI preparations of

Petromyzon ('02), though the secondary neurones of type I
were found about as in teleosts. It Petromyzon, it is interest-
ing to note in this connection, the cutaneous terminal bud sys-
tem is well developed.
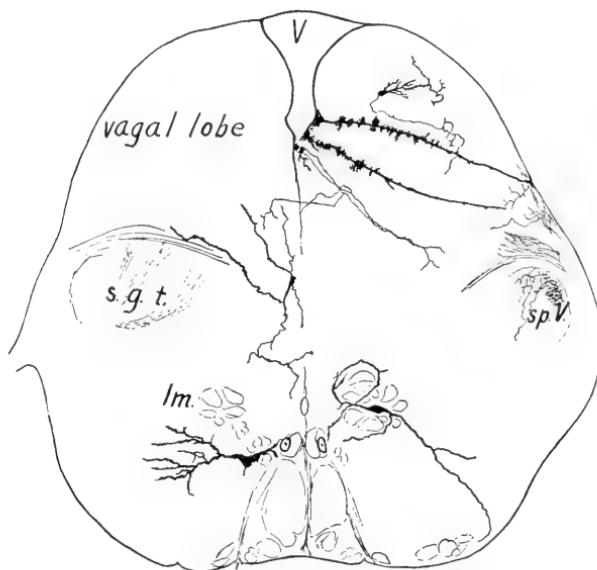
Fig. 29. Transverse section through the vagal lobes of *Ameiurus nebulosus*
illustrating a type II cell within the vagal lobe similar to those in Figs. 27 and
28; also two other small cells at the ventral angle of the fourth ventricle, whose
neurites terminates among the intermediary neurones of the same and opposite
side. One of the latter cells is impregnated; also a ventral horn cell on the left
side. Two supporting fibers of the neuroglia system are shown on the right side.
GOLGI method. × 50.

l.m., lemniscus; *s.g.t.*, secondary gustatory tracts; *sp.V.*, spinal V tract;
V., ventricle.

The root fibers which end on the surface of the vagal lobe
spread out in very wide arborizations (Figs. 30 and 31). These
are most densely massed in two regions in intimate relation with
the two groups of chief secondary neurones already referred to
as the dorsal and lateral secondary gustatory neurones (Fig. 26).
The general relations of the two groups of superficial secondary
neurones are indicated in Fig. 31, where a dense neuropil richly

impregnated indicates the positions of these two chief centers of secondary connection for gustatory root fibers.
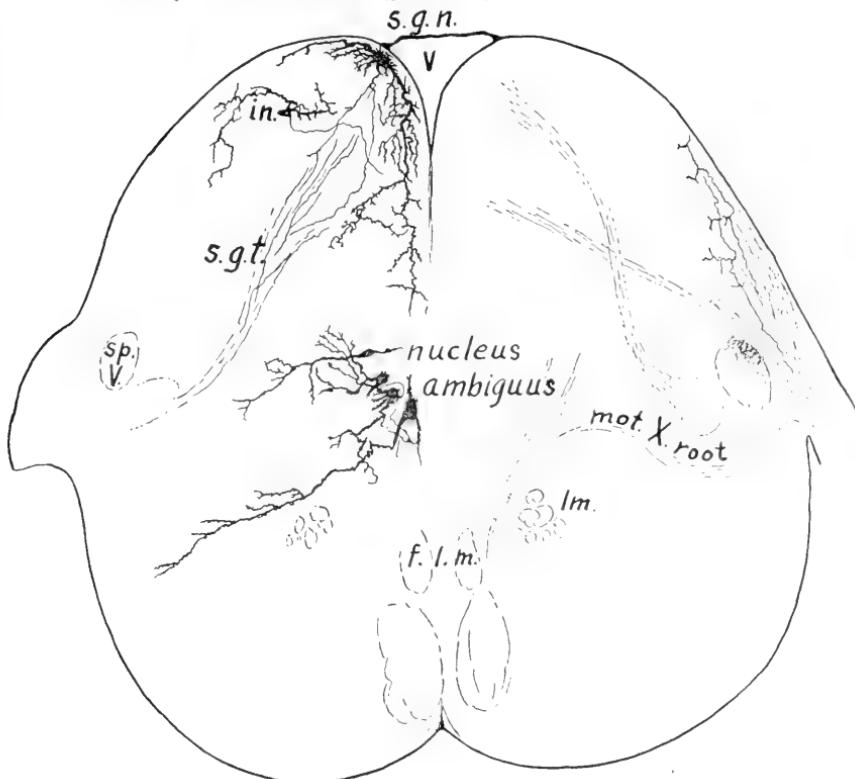
Fig. 30. Transverse section through the vagal lobes of *Ameiurus nebulosus.* Golgi method. ×60.

On the left side is shown a gustatory neurone of the dorsal secondary group (*s.g.n.*), whose neurite enters the secondary gustatory tract (*s.g.t.*). The preparation shows one of the intrinsic neurones of the vagal lobe (*in.*), also several cells of the nucleus ambiguus. On the right side are seen some of the simpler terminations of the communis root of the vagus.

The dorsal portion of the superficial roots of the vagus and glossopharyngeus is the most important member of the complex. Its fibers arborize intimately intertwined with the thick thorny dendrites of the dorsal secondary neurones (Figs. 30, 31, 32). These are very highly differentiated cells whose neurites arise from the cell body and constitute the secondary gustatory tract, or central gustatory path. Their dendrites are
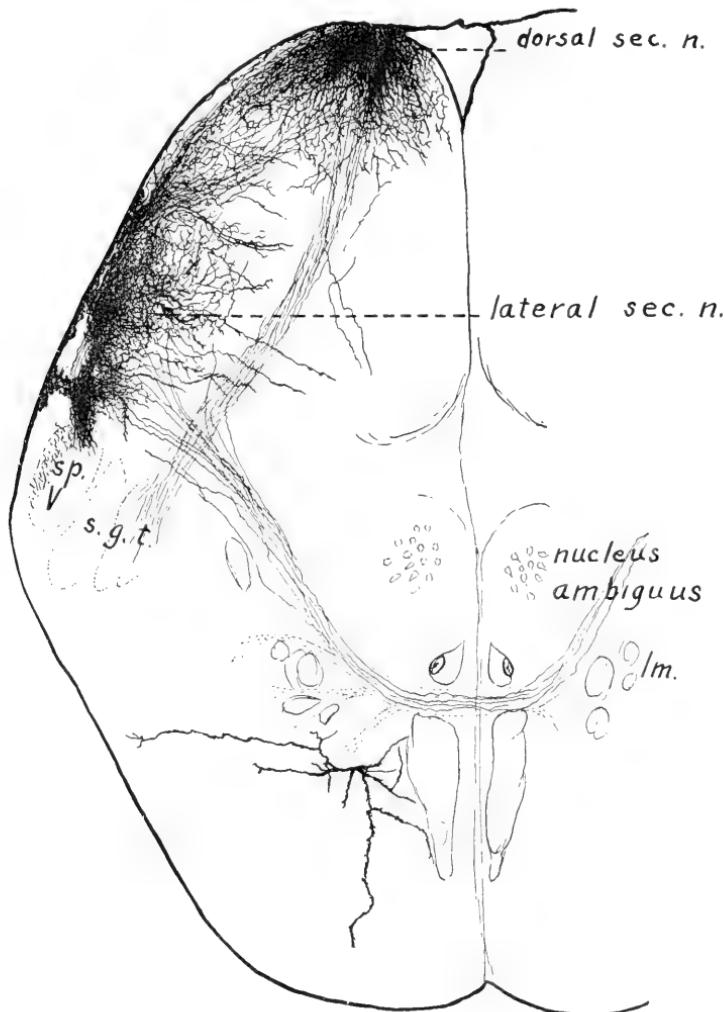
Fig. 31.   Transverse section through the cephalic part of the vagal lobes of *Ameiurus nebulosus.*   From a GOLGI preparation.   × 90.

It illustrates the general relations of the termini of the gustatory fibers of the vagus.   Dorsally these root fibers form dense arborizations about cells of the dorsal secondary group of the vagal lobe (*dorsal sec.n.*), and ventrally about cells of the lateral secondary group (*lateral sec.n.*).   From the dorsal group neurites pass downward and outward into the secondary gustatory tract (*s.g.t.*); from the lateral group neurites pass to the opposite side through the ventral commissure (cf. Fig. 33).

very thick, thorny and much branched, interlacing with the root fibers to form a very dense neuropil in the most superficial layer of the vagal lobe.
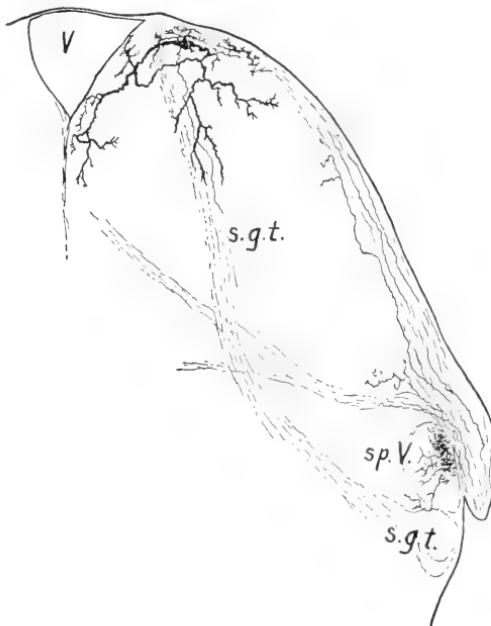
Fig. 32. Transverse section through the vagal lobe of *Ameiurus nebulosus,* illustrating a secondary gustatory neurone similar to that shown in Fig. 30. GOLGI method. × 60.

As the figures show, they are very unlike the corresponding cells of the vagal lobe of the larger cyprinoid fishes, whose minute cell bodies are closely crowded around the periphery with the bushy dendrites thrust directly inward and giving off at the apex the neurite. These cells are exceedingly numerous in the carp and relatively few in the cat fish, and this fact doubtless explains the difference in form. Probably neither type is very near the primitive form. JOHNSTON figures in his Petromyzon paper ('02, Figs. 7 and 21) chief cells of the vagal lobe of Lampetra whose cell bodies lie close to the ventricle and give off the neurite directly, while the busy dendrite is directed toward the periphery. HOUSER ('01) unfortunately secured no impregnations of the chief gustatory cells of the shark, his prep-

arations showing only the intrinsic type II cells.   In Acipenser
JOHNSTON ('01) finds these cells similar to my impregnations of
the cyprinoids, but much simpler.
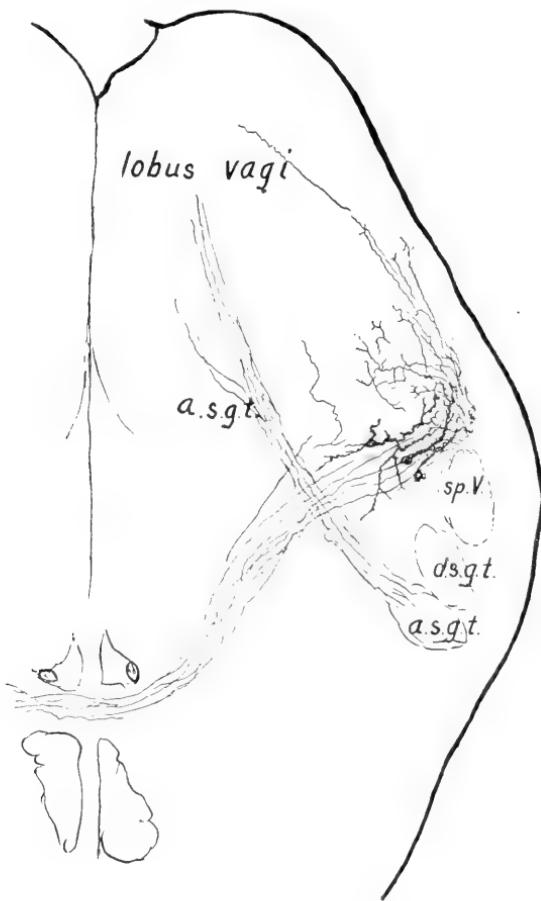
Fig. 33.   Portion of a transverse section through the oblongata of *Ameiurus
nebulosus* in the cephalic part of the vagal lobe.   From a GOLGI preparation.
× 90.
    The section illustrates terminal arborizations of the most cephalic fibers of
the gustatory root of the vagus among the dendrites of the neurones of the later-
al secondary group and the course of the neurites from the latter through the
raphé toward the substantia reticularis of the opposite side.   *a.s.g.t.*, ascending
secondary gustatory tract from vagal lobe ; *d.s.g.t.*, descending secondary gusta-
tory tract from facial lobe ; *sp. V.*, spinal V tract.

The neurites from the cells of the lateral secondary gustatory nucleus are in the main directed across the raphé through the ventral commissure to reach the substantia reticularis grisea of the opposite side of the oblongata (Figs. 31, 33). Here they may come into relation with the dendrites of the nucleus ambiguus and other motor nuclei. They are to be regarded as direct reflex paths, differing from those provided by the intermediary neurones in that there is no type II cell interpolated between the root fiber and the tract neurone. Since this arrangement prevails also for the main ascending gustatory path, it is probable that this is the path of direct motor reflexes excited by the gustatory communis root fibers rather than by the unspecialized visceral element.

The dorsal and lateral groups of chief secondary neurones receive by far the greater part of the vagal communis root fibers, and since most of these root fibers are gustatory in function, we may infer with great confidence that the more lateral group of secondary neurones is the chief path for direct gustatory reflexes in the medulla oblongata and spinal cord, while the more dorsal group is the main ascending or central gustatory path.

Neurites from the dorsal group of secondary neurones pass through the middle of the vagal lobe in slender compact bundles, directed downward and outward to a position ventrally of the spinal V tract. Here they turn and take a longitudinal direction, most turning cephalad and constituting the ascending secondary gustatory tract ("sekundäre Vagusbahn," MAYSER), but some caudad. The latter are derived chiefly from the more lateral part of the vagal lobe and more probably should be relegated to the cells of the more lateral group of neurones. The relations of the ascending fibers from the vagal lobe and both the ascending and the descending fibers from the facial lobe are indicated in Fig. 37.

The relations of the cells of the intermediary nucleus of the vagal lobe are not very clearly brought out in my preparations. Figs. 29 and 34 show their dendrites in relation with the neurites of type II cells of the vagal lobe. Some prepara-

tions suggest that the neurites of these cells end in relation with cells of the nucleus ambiguus. Other preparations show their neurites extending out into the substantia reticularis (right side of Fig. 34), and still others show their neurites passing into the decussating tract for the ventral commissure, probably for the
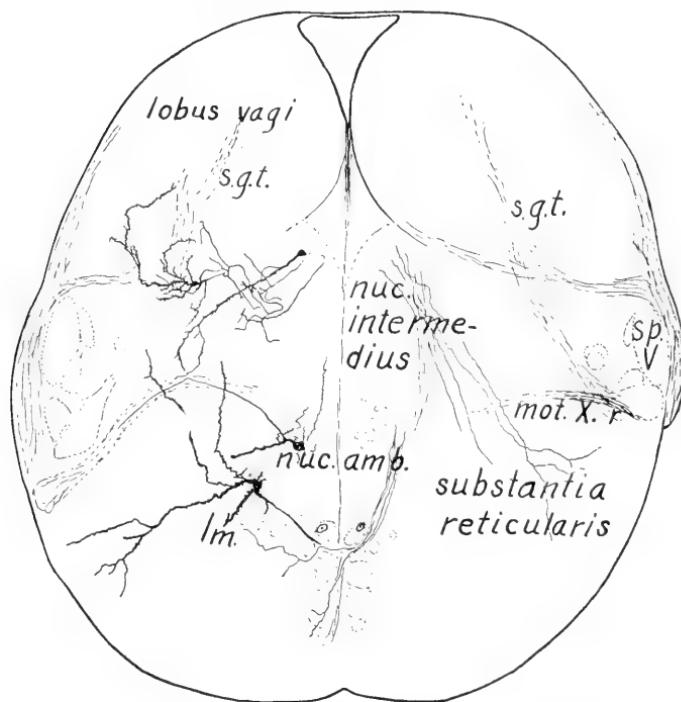
Fig. 34. Transection through the vagal lobes of *Ameiurus melas.* GOLGI method. × 50.

The figure shows on the left an intrinsic neurone whose neurite (of type II) arborizes in the nucleus intermedius. One neurone of the latter nucleus is impregnated, though only the proximal part of the neurite is shown. On the opposite side similar neurites are seen to enter the substantia reticularis grisea and the tract for the ventral commissure.

substantia reticularis of the opposite side. Completely impregnated neurones of the latter type are figured by VAN GEHUCHTEN ('94, Plate I, Fig. 13) for the trout. Some of these neurites reach the level of the commissura infima Halleri and arborize among the cells of the commissural nucleus of CAJAL. In

this way are provided extensive pathways for vagus reflexes both of the gustatory and unspecialized visceral type. This layer of intermediary neurones extends caudad from the vagal lobes directly into the commissural nucleus and the latter is probably in part a differentiation from it. The motor layer of the vagal lobe of cyprinoids occupies the position corresponding to these intermediary neurones, but the structures are not exactly equivalent. These cells are probably represented in the carp by intrinsic neurones which send their neurites into the substantia reticularis. I have no preparations of Ameiurus showing motor root fibers springing from this nucleus, such as arise from the motor layer of the vagal lobe of the carp. Here, as in the cyprinoids, there is no direct path between the termini of the primary gustatory root fibers and the motor nuclei of the oblongata. The most direct return reflex path is by way of the nucleus ambiguus whose neurites pass directly out to the striated branchial musculature. But the dendrites of these cells in no case come into relation with the termini of sensory root fibers. On the other hand, they ramify in the substantia reticularis (Fig. 30) and at least one neurone is always intercallated between them and the sensory root fibers. A similar relation prevails for the connections with the other motor nuclei.

The *facial lobes* of Ameiurus are considerably larger than the vagal lobes and each is incompletely divided into mesial and lateral lobules by a shallow fissure. Both lobules receive the terminals of the very large communis root of the facial nerve, this root entering the lobus from in front at its ventrolateral border and spreading out in many strands which pass upward through the lobe to reach its exposed surfaces. The internal structure is in general similar to that of the vagal lobes. There are numerous very small intrinsic neurones and larger secondary neurones bordering the surface, which differ somewhat in form from those of the vagal lobe.

Fig. 35 shows some of the simpler types of endings of the root fibers. The interior of the lobe in occupied by intrinsic neurones of type II which are similar to those of the vagal lobe (Fig. 35 *in.*). The secondary connections are likewise essen-

tially similar. The large tract of descending neurites shown in Fig. 37 passing from the facial lobe arises from the lateral part of the lobe, while the ascending secondary tract, or central gustotory path, takes its origin from the more mesial portion of the dorsal surface. These chief gustatory neurones of the facial lobe are like those of the vagal lobe in staining reaction, position and general relations. They are, however, smaller with more slender dendrites. One of them is shown in the dorsal
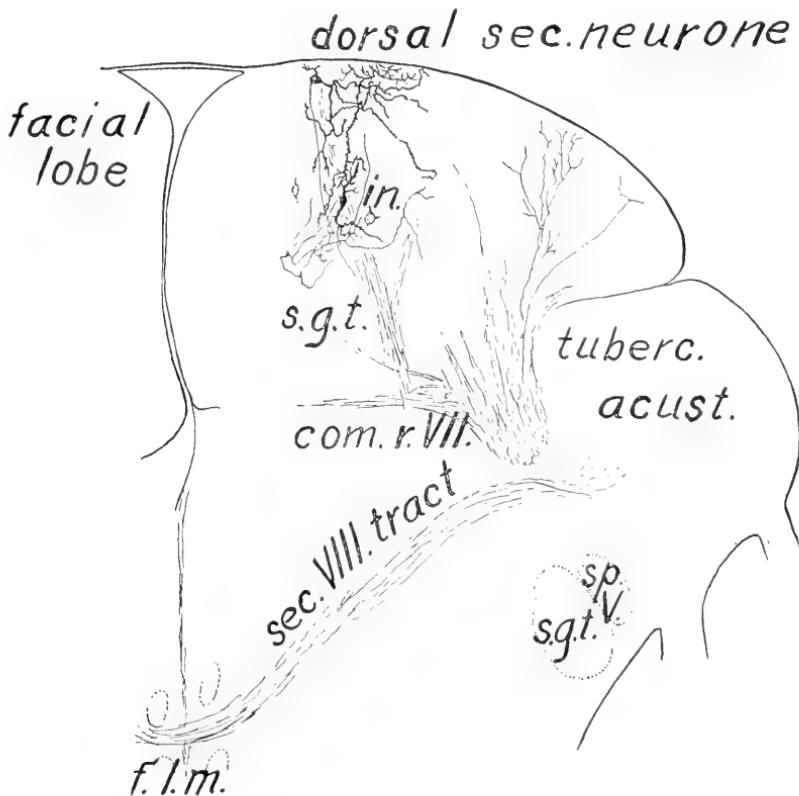
Fig. 35. Portion of a transection though the cephalic end of the right facial lobe of *Ameiurus nebulosus*. GOLGI method. × 60.

The communis (gustatory) root of the facialis (*com.r. VII.*) enters from below. Dorsally is a single impregnated chief secondary neurone whose neurite enters the secondary gustatory tract (*s.g.t.*), and below it is an intrinsic neurone of type II (*in.*).

part of Fig. 35 and another as seen from above in horizontal section in Fig. 36. Ventro-mesially of the facial lobe, especially its caudal part, is a region of sparse cells which extends caudad to join the intermediate nucleus of the vagal lobe. It will be termed the intermediate nucleus of the facial lobe and is strictly comparable with the corresponding region of cyprinoids.
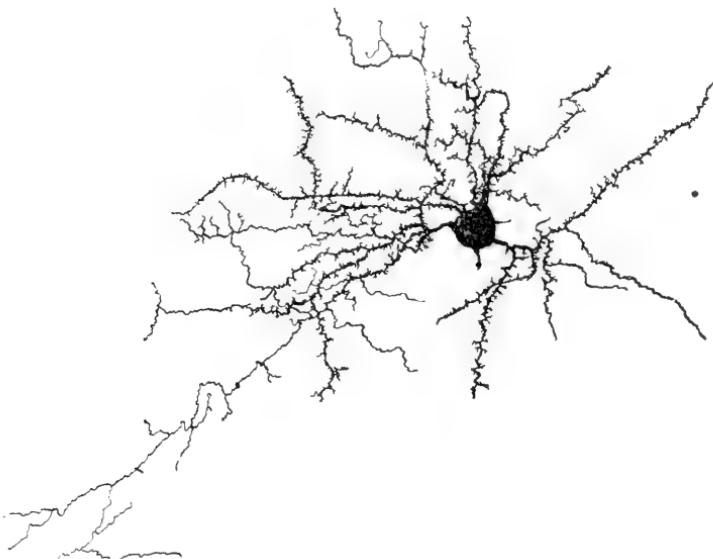
Fig. 36. A secondary neurone of the dorsal part of the facial lobe of Amei-urus as seen from above. GOLGI method. × 500.

Drawn from a horizontal longitudinal section passing through the extreme dorsal part of the facial lobe. The neurite extends ventrally at right angles to the plane of the section (cf. Fig. 35) and hence of course does not appear in this preparation.

The greater part of the chief gustatory neurones of the vagal and facial lobes, as we have seen, send their neurites into the ascending secondary gustatory tract, or central gustatory path (secondary vagus bundle of MAYSER). This ascending tract terminates in the secondary gustatory nuclei under the cerebellum, partly on the same side and in smaller numbers on the opposite side. These nuclei lie in the isthmus close under the cerebellum at the point where the body of this organ is joined by the valvula cerebelli. The two nuclei are connected

by a broad dorsal commissure, above which is a commissure of the acustico-lateralis centers lying under the lateral extensions of the cerebellum. They are enveloped on all sides by tracts of fibers running vertically between the cerebellum and the regions in the brain stem below and cephalad of the nuclei, the cerebellar tracts forming a sort of capsule around the grey nuclei, these relations being the same as already described for cyprinoids. The relations of this nucleus and its tracts are shown in Fig. 37.

The intrinsic neurones of these nuclei are rarely well impregnated in my GOLGI preparations. The fibers of the central gustatory path end for the most part in free arborizations among these cells without crossing. But some of the tract fibers are clearly seen to cross to the opposite nucleus through the commissure of the secondary gustatory nuclei, as MAYSER has stated.

The tertiary tract arises from the chief cells in the cortical portions of the nucleus. These are frequently impregnated

Fig. 37. A parasagittal section taken through the brain of *Ameiurus nebulosus* so cut as to pass through about the middle of one vagal and one facial lobe and the lateral part of the cerebellum (cf. Figs. 5 and 20). Drawn from a single GOLGI preparation. × 45.

The section shows nearly the whole course of the central gustatory path (*sec.gust.t.*), composed of neurites of the chief secondary gustatory neurones of the vagal and facial lobes which terminate in the secondary gustatory nucleus (*s.g.n.*) under the cerebellum. The origin of the facial portion of the descending secondary gustatory tract (*desc.sec. VII.*) is seen in the facial lobe. In the facial lobe there is also seen a portion of the lateral part of the communis root of the facial nerve (*com. VII*) passing up to arborize within the lobe. The neurones of the vagal and facial lobes, which were richly impregnated in the preparation, are omitted from the drawing for the sake of simplicity. Along the cephalic border of the secondary gustatory nucleus is the beginning of the secondary gustatory commissure (*s.g.c.*). The origin of the tertiary gustatory tract from the secondary nucleus is not shown, but the terminations of these fibers (*gust.3*) are illustrated in the inferior lobe.

Bundles of fibers from the tuberculum acusticum are seen under the facial lobe, where they decussate, and their termini in the nucleus lateralis mesencephali (torus semicircularis or colliculus) are also shown (*sec. VIII*). Under the cerebellum are the cerebellar tracts which envelop the secondary gustatory nucleus (*c*). Granules of the cerebellum are marked *gr.*; those of the valvula, *g*. The bodies of the Purkinje cells of the cerebellum are indicated by dotted outlines. *nuc.com.*, is the commissural nucleus of CAJAL.
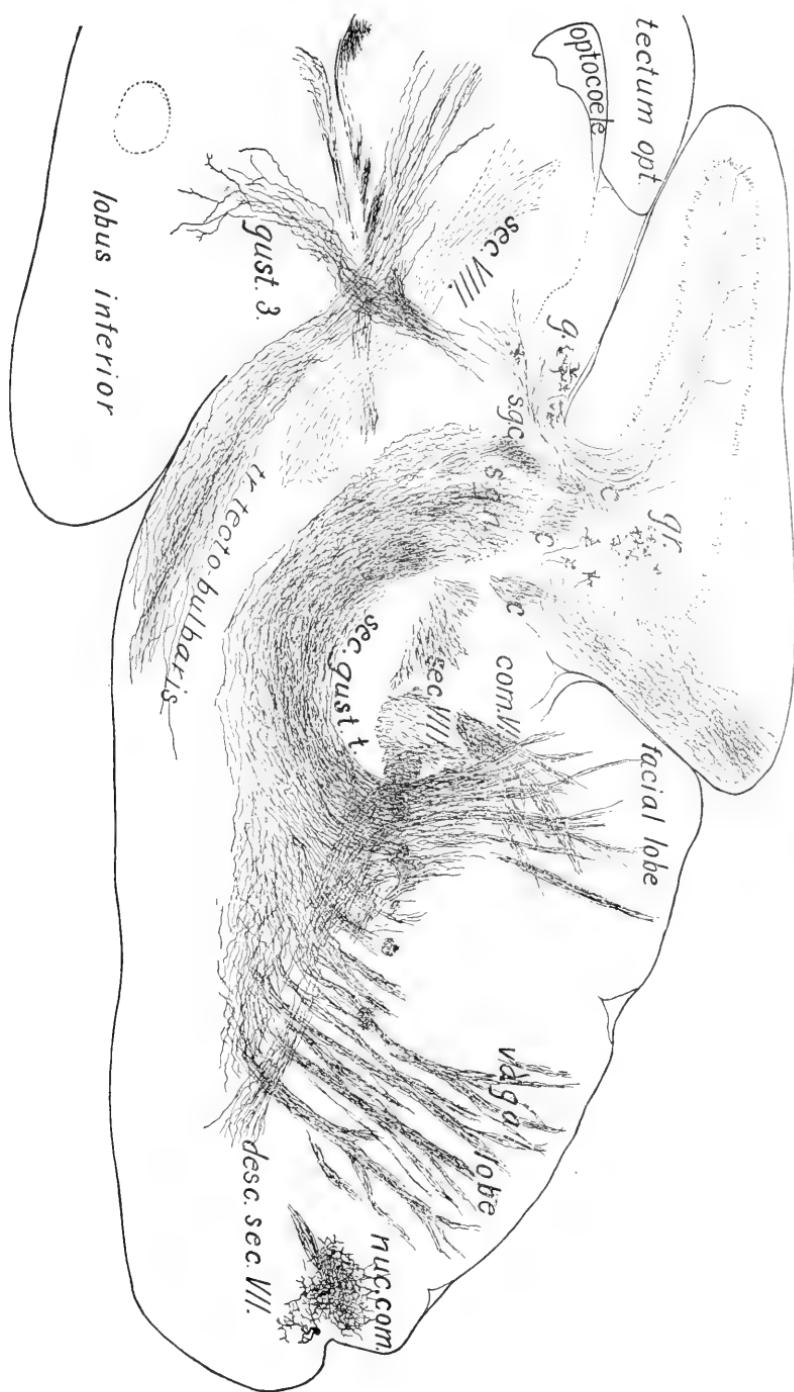
and are of the same type as in cyprinoids. Their neurites, mingling with the tractus lobo-cerebellaris, pass down to end in the inferior lobe of the same side, essentially as already described for the carp. The ventral portion of this tract and its terminal arborizations are seen in Fig. 37.

The return path in the oblongata by way of the tractus lobo-bulbaris is also essentially as described for the carp.

SECTION V.   SUMMARY AND GENERAL CONCLUSIONS.

In this section a brief summary of the facts as described in the preceding pages is followed by a discussion of some of the morphological considerations growing out of them.

The teleostean fishes generally possess taste buds freely scattered over the mucous surfaces of the mouth, gills and lips. The group of Ostariophysi is characterized by a very great development of this system of sense organs—in the siluroids in the outer skin and barblets and in the cyprinoids both in the outer skin and in still greater degree in the palatal organ within the mouth.

It has previously been shown experimentally that these fishes do in reality taste with their cutaneous taste buds, which are often called terminal buds and which have no relationship whatever with any variety of lateral line organs. Furthermore, while pure cutaneous gustatory stimuli can be localized by the fish, ordinarily both gustatory and tactile stimuli cooperate in the discrimination and localization of food objects.

The distribution and innervation of the organs of taste have been accurately determined for the siluroid fish, Ameiurus, all of them being innervated by the communis system of peripheral nerves. The nerves from the buds in the outer skin enter the brain exclusively by the facialis root ; those from within the mouth by the facialis, glossopharyngeus and vagus roots, chiefly the latter. A special tuberosity of the brain, the lobus vagi, serves in fishes generally as the primary cerebral center for all gustatory nerves. This is greatly enlarged in some cyprinoids to provide for the taste buds in the palatal organ, and in both cyprinoids and siluroids there is another tuberosity de-

veloped, the lobus facialis, which receives all the gustatory nerves from the outer skin.

The purpose of this study is to trace the farther course of these gustatory pathways within the brain and in particular to map out the reflex paths for the various types of gustatory reaction which have been actually observed in the feeding activities of these fishes.

Peripheral gustatory nerve fibers (especially those of the X and IX nerves) enter the brain in company with unspecialized visceral sensory fibers from which they can be distinguished within the brain only with difficulty. This mixed system is spoken of as the communis system of nerves and centers. It is probable that the complete analysis of this complex can be made only by the degeneration method. But the comparative method has enabled us to determine with great probability the chief secondary connections of both types of fibers and so to prepare the way for an accurate determination of the gustatory pathways in the human brain, which are at present almost wholly unknown.

In the cyprinoids and siluroids the primary gustatory centers possess in both the facial and the vagal lobes two types of secondary neurones ; (1) small intrinsic neurones (largely of GOLGI's type II) filling the interior of the lobe, and (2) larger and very highly specialized neurones superficially arranged over the lobes—the chief secondary gustatory neurones.

The intrinsic neurones serve to diffuse incoming stimuli throughout the substance of the lobes and those with longer neurites effect connections with adjacent motor areas, chiefly by way of the substantia reticularis grisea. These connections are probably very largely for unspecialized visceral sensory reflexes, as well as for direct response of the mandibular branchial and palatal musculature (muscles of the visceral system) to gustatory stimulation, and are probably substantially similar in all vertebrates.

The chief gustatory neurones of both vagal and facial lobes give rise to the long paths of secondary connection for distant parts of the brain. Their dendrites receive directly the per-

ipheral gustatory terminals of the first order and their neurites either descend to the inferior secondary gustatory nucleus in the region of the funicular nuclei or ascend to the superior secondary gustatory nucleus in the isthmus. In both cases the path is mainly and perhaps exclusively gustatory in function.
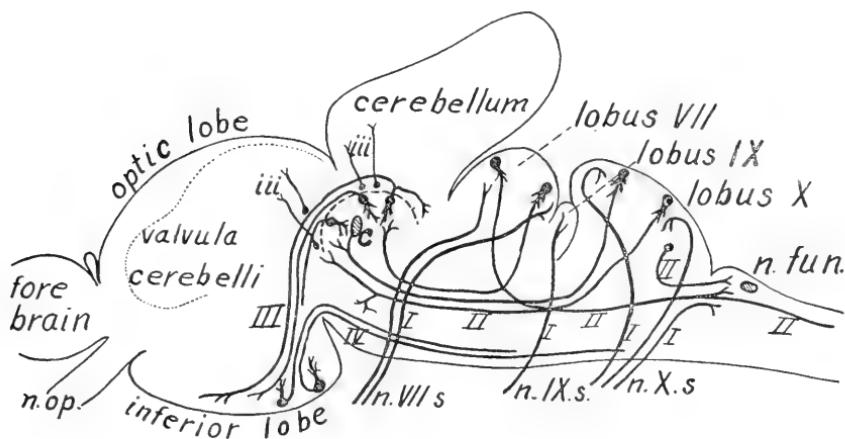
Fig. 38. Diagram of the gustatory paths in the brain of the carp as seen from the side. Only the long paths are shown in this diagram (cf. Fig. 39).

n.VII.s., n.IX.s., and n.X.s., represent the sensory root fibers of the facialis, glossopharyngeus and vagus respectively, or gustatory neurones of the first order (*I*). The secondary tracts, both ascending and descending, are marked *II*. The tertiary path to the inferior lobe is marked *III*; the path to the cerebellum and valvula, *iii*. The return path from the inferior lobe to the motor nuclei of the oblongata (tractus lobo-bulbaris) is marked *IV*. The commissures of the inferior and superior secondary nuclei are indicated by shaded areas (the latter marked *c*). *n.op.,* the optic nerve. The area marked *n.fun.* includes the funicular nucleus and the inferior secondary gustatory nucleus.

In cyprinoids the gustatory neurones of the smaller type proba-bly share both this function and that of the intrinsic neurones. In no case does a peripheral gustatory neurone connect directly with a peripheral motor neurone. There is always at least one intermediate neurone between them.

The vagal lobes of the larger cyprinoids differ from those of the siluroids, in addition to the points already mentioned, in the following respects: (1) The chief secondary neurones, being exceedingly numerous and crowded in a narrow peripheral

layer, thrust their dendrites inward in a radial direction and there engage the termini of the peripheral neurones of the first order instead of spreading out tangentially among these termini, and the neurite arises from the tip of the dendrite. This ar-
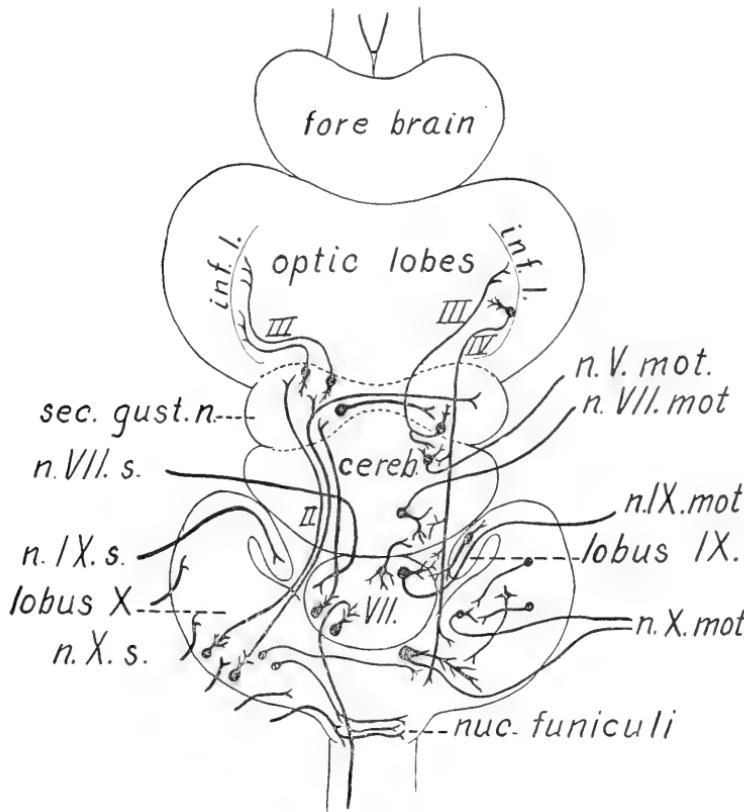
Fig. 39. Diagram of the gustatory paths in the brain of the carp as seen from above. Designations in general as in Fig. 38.

The sensory root fibers and long sensory tracts are indicated on the left side; the short paths, return path from the inferior lobe and motor root fibers, on the right side. The lines, *inf.l.*, designate the outer margins of the inferior lobes. The dendrites of all the motor nuclei ramify in the substantia reticularis grisea. Two types of motor fibers are indicated in the vagus root (*n.X.mot.*), (1) those from the motor layer of the vagal lobe (above), and (2) those from the nucleus ambiguus (below). The facial lobe is designated, *VII*; the superior secondary gustatory nucleus, *sec.gust.n.* The area designated *nuc.funiculi* contains also the inferior secondary gustatory nucleus.

rangement is probably merely a device for economy of space (cf. Figs. 10 and 30). (2) The deepest cells of the vagal lobe are motor neurones (probably derived phylogenetically from the underlying nucleus ambiguus and related to the dorsal motor nucleus of the vagus of FOREL *et al.*) which supply directly the intrinsic muscles of the palatal organ. These motor cells are not present in recognizable numbers in siluroids or other teleosts—correlated with the absence of the palatal organ. (3) A large proportion of the intrinsic neurones serve as intermediaries between the peripheral termini and the motor layer of the vagal lobe, thus providing for a reflex connection within the lobe between the taste buds on the palatal organ and the intrinsic muscles of that organ.

The main paths of gustatory conduction in these fishes may be summarized as follows (cf. the accompanying schemata, Figs. 38 and 39.)

A. Short Paths.

1. Impulses originating in taste buds on the palatal organ pass by way of the X and IX nerves to the vagal lobe; then through the intrinsic neurones to the motor layer and the intrinsic muscles of the palatal organ (in cyprinoids only).

2. From peripheral termini in both the vagal and facial lobes to the substantia reticularis of the same side via intrinsic neurones, the smaller type of marginal neurones (in cyprinoids) and collaterals of the chief neurones. These neurones of the second order, either directly or through the mediation of tertiary neurones of the substantia reticularis grisea, reach the dendrites of the visceral motor nuclei of the medulla oblongata. This provides a pathway for reflex movements of the lips, barbels, tongue, jaws, gills and pharynx in response to gustatory stimulation.

3. Some of the chief gustatory neurones send their neurites directly across the raphé, probably to end in the substantia reticularis of the opposite side of the oblongata. There is also, of course, indirect connection between the substantia reticularis of the two sides of the body, thus providing for coordinated action of the muscles of both sides.

4. The nucleus intermedius of the vagal lobes and the associated substantia reticularis extend caudad from their lobes to fuse directly with important gustatory centers lying mesially of the funicular nuclei—the inferior secondary gustatory nuclei. These nuclei are connected by the commissura infima HALLERI and the commissural nucleus of CAJAL is a specialized part of this gustatory center. These nuclei are very intimately related to the funicular nuclei and thus afford a mechanism of correlation between gustatory and tactile impressions.

B. Long Paths.

5. The descending secondary gustatory tract arises from the chief gustatory cells of the facial lobe mainly and terminates partly in the inferior secondary gustatory nucleus and a smaller part lower down in the spinal cord. This puts the taste buds in the outer skin into very direct relations with the trunk musculature and so provides for the body movements necessary to turn and seize food after its detection by contact with cutaneous taste buds. This inferior nucleus, as stated above, is connected by a rich fibrous plexus with the funicular nucleus, which is the primary tactile coordination center for the skin of the head and trunk. Thus the cutaneous gustatory and tactile impressions may be brought into relation, as required by the physiological evidence that these senses cooperate in the localization of food objects.

6. The ascending secondary gustatory tract arises from the chief secondary neurones of both vagal and facial lobes and terminates in the superior secondary gustatory nucleus located in the lateral wall of the isthmus (the "Rindenknoten" of MAYSER). It ends chiefly on the same side, but a part of its fibers cross through the commissure of the secondary nuclei to end in the opposite nucleus.

The superior and inferior secondary gustatory nuclei are both specializations of the substantia reticularis grisea. The superior nucleus is especially intimately connected with the motor V nucleus, partly directly and partly through another specialized area termed the substantia reticularis grisea trigemini. It also has connections cephalad with the region of the eye-muscle nuclei and the nucleus of the fasciculus longitudinalis medialis, thus putting the gustatory system into physiological relation with the somatic motor centers. There is also probably an important connection between the superior nucleus and the cerebellum and valvula cerebelli by way of the nucleus lateralis valvulae. These important mesencephalic and cerebellar connections merit much more thorough study.

7. The chief tertiary gustatory tract arises from cells in the cortical layer of the secondary nucleus, whose dendrites receive the terminal arborizations of the secondary fibers. This tract is heavily medullated and mingles with the tractus lobo-cerebellaris (EDINGER) and other vertical tracts connecting with the cerebellum, so that it is difficult to follow it separately. GOLGI impregnations show that its fibers pass ventrad and slightly cephalad to arborize widely throughout the lateral lobule of the inferior lobe (hypoaria, C. L. HERRICK) along with others from the forebrain, tectum, etc. This appears to be the chief center for the correlation of olfactory and other higher senses.

8. The return path for all of these sensory activities of the inferior lobe is the tractus lobo-bulbaris, the dendrites of whose cells of origin ramify widely among the gustatory and other terminals just mentioned. This tract (MAYSER'S "Nervenfaser-bundel x") passes into the oblongata mesially of and partly enclosed by the ascending secondary gustatory tract and along the lateral border of the substantia reticularis grisea, within which its fibers gradually diffuse themselves. Through the medium of this reticular area the descending impulses from the inferior lobe come into relation with the peripheral motor neurones of the oblongata and probably also of the spinal cord, thus providing for the most complex reflexes of which the fish is capable.

TABLE OF THE GUSTATORY PATHS IN FISHES.

A. PERIPHERAL NEURONES—GUSTATORY NEURONES OF THE FIRST ORDER.

    I. Radix communis facialis.

    II. Radix communis glossopharyngei.

    III. Radix communis vagi.

        These radices contain unspecialized splanchnic fibers in addition to gustatory fibers. In their intra-medullary courses they unite to form the fasciculus communis of the Ichthyopsida, or the fasciculus solitarius of birds and mammals. In some animals the secondary gustatory fibers are also in part represented in this tract.

B. NUCLEUS GUSTUS PRIMUS.

        The communis roots terminate in a medullary center which may be termed the primary communis center. That portion of this center which receives the gustatory component of these roots is the primary gustatory nucleus. It may be single, but in the fishes described in this paper is double.

    I. Lobus Vagi.

        1. Layer of root fibers.

        2. Layer of secondary neurones.

            1) Chief secondary neurones.

            2) Intrinsic secondary neurones.

        3. Layer of secondary gustatory tracts.

        4. Layer of motor neurones.

        5. Ependyma.

            These layers occur as above only in some cyprinoids. In place of the 4th layer in siluroids is the nucleus intermedius vagi, and in these fishes the chief gustatory neurones are arranged in dorsal and lateral groups with somewhat different secondary connections.

    II. Lobus facialis (=tuberculum impar=lobus trigemini, MAYSER).

        1. Chief secondary neurones.

        2. Intrinsic secondary neurones.

        3. Nucleus intermedius facialis.

    III. Lobus glossopharyngei (in cyprinoids only).

C. TRACTUS GUSTUS SECUNDUS DESCENDENS.

        1. Pars facialis (distinct only in cyprinoids and siluroids).

        2. Pars vagi (part of the spinal portion of the fasciculus solitarius in mammals).

D. TRACTUS GUSTUS SECUNDUS ASCENDENS (central gustatory tract = "sekundäre Vagus-Trigeminusbahn," MAYSER).

        1. Pars facialis (in cyprinoids and siluroids only).

        2. Pars vagi.

E. NUCLEUS GUSTUS SECUNDUS INFERIOR.

F. NUCLEUS GUSTUS SECUNDUS SUPERIOR (central gustatory nucleus = "Rindenknoten," MAYSER=secondary vagus nucleus, JOHNSTON).

        1. Commissure of secondary gustatory nuclei.

        2. Intrinsic neurones (mainly commissural ?).

3. Chief tertiary gustatory neurones.
G. TRACTUS GUSTUS TERTIUS.
    1. Ad lobum inferiorem.
    2. Ad cerebellum.
    3. Ad mesencephalon.
    4. Ad substantiam reticularem.

A detailed discussion of the *mammalion homologies* of the tracts and nuclei enumerated in the preceding table is as yet premature. Much further work on the intermediate types remains to be done before such comparisons can have much value except as suggestions for further research.

In the human body the lingual branch of the glossopharyngeal nerve (from taste buds at the base of the tongue) undoubtedly corresponds to a portion of the pre-trematic branch of the same nerve in fishes. The course of the peripheral gustatory nerve from the taste buds at the tip of the tongue is still disputed, though the evidence is rapidly accumulating that this course is via the lingual nerve, chorda tympani and portio intermedia of WRISBERG into the fasciculus solitarius. The homologies of the chorda tympani have given comparative anatomists a world of trouble. If the gustatory component of the chorda in man supplies taste buds on the tip of the tongue, it is obvious that in the fishes there can be no strictly homologous nerve, for there is no fleshy tongue in fishes. From what branch of the piscine facial nerve the mammalian chorda tympani has been specialized is uncertain—possibly from none of them.

The identification of the fasciculus communis of amphibia with the fasciculus solitarius of mammals was a very important step in advance. In the teleosts the case is much more complicated and difficult of correlation. But the descriptions of CAJAL ('96, p. 43) permit comparisons which are very close in all fundamental respects. In the new-born mouse there is a single sensory root for the vagus and glossopharyngeus and a single terminal nucleus which is the grey substance associated with the fasciculus solitarius. In addition to the dorsal nucleus of KÖLLIKER, which is a specialized portion of this substance, there is another and more important specialization from it in the

region of the funicular nuclei. Here is a commissure which corresponds to the commissura infima HALLERI of teleosts and a commissural nucleus which is also present in fishes and which is closely related to the inferior secondary gustatory nucleus of my descriptions. In the mouse the greater part of the primary sensory root fibers of the IX and X nerves appears to end in this nucleus; in the fishes a very small part, while the greater part of the fibers end in the vagal lobe whose sensory portion is homologous with the dorsal sensory nucleus of KÖLLIKER. The commissural nucleus of CAJAL, as a primary end-station for the spinal root of the vagus, is homologous with the terminal nucleus of the descending vagus root fibers associated with the inferior secondary gustatory nucleus. The latter nucleus is not represented in CAJAL's descriptions, though I venture the prediction that further study of the mammals will show that it too is represented in the commissural nucleus. CAJAL finds that the neurites of the cells of the commissural nucleus enter the lemniscus along with secondary tracts from the funicular nuclei (secondary tactile path), and here again the teleostean and mammalian relations are closely parallel.

His has shown that the fasciculus solitarius, when first apparent in the human embryo, lies, like the spinal V, superficially on the lateral border of the oblongata and its deeper adult position is due to the overgrowth of structures from the ''Rautenlippe.'' In teleosts it lies still deeper, as close to the median line as possible. This may be explained by the fact that the fasciculus solitarius as a visceral sensory tract is more ancient than the specialized somatic sensory enlargement (tuberculum acusticum) of this part of the oblongata. The communis VII + IX (= fasc. communis) was therefore passively crowded inward from the primitive superficial position by the over-growth of the tuberculum acusticum (and later by the ''Rautenlippe'' for the olive) and prevented from passing ventrally by the great ventro-lateral tracts and the secondary mechanism for the tuberculum acusticum. The spinal V tract, however, being organically connected with the somatic sensory centers here develop-

ed, retained its superficial position with reference to them. In
passing from the fishes to the mammals the fasciculus solitar-
ius has been crowded again somewhat laterally on account of
the further development of median structures.

The short gustatory paths between the primary centers
and the motor nuclei of the oblongata by way of the substantia
reticularis are essentially the same in the fishes and mammals.

The homology of the nucleus ambiguus of fishes and mam-
mals is not open to question. FOREL in 1891 showed that the
so-called chief or dorsal sensory nucleus of the IX and X nerves
of mammals is in reality a motor nucleus of origin for these
nerves and much evidence in confirmation of this view has since
been published. The motor layer of the vagal lobe of cyprin-
oids corresponds in position exactly with this nucleus and is
probably in a broad way homologous with it, though of course
the homology is not exact.

The long ascending secondary tracts from the vagal and
facial lobes (central gustatory path, or tractus secundus ascen-
dens) has not been identfied in any vertebrates save the fishes,
though it has long been in the minds of several neurologists
that the homologies of this tract are to be sought in the lateral
cerebellar tract of FLECHSIG (tractus spino-cerebellaris dorsalis,
EDINGER). These fibers are known to arise from the cells of
CLARKE'S column (supposed to be a visceral sensory center)
and to enter the vermis cerebelli by way of the restiform body
of the same side. Dorsally of the ventricle they cross to the
opposite side and the whole arrangement strongly suggests a
survival of a primitive secondary tract from the visceral sensory
center of the spinal cord to the isthmus, to which in fishes the
strong secondary gustatory tracts arising in the oblongata are
added. This suggestion, however, cannot be taken seriously
until we have much more exact knowledge of the superior con-
nections of these fibers in the mammals and of the comparative
anatomy of the structures at the base of the vermis cerebelli.

The morphological relations of the secondary gustatory
tract and nucleus are clearly defined. The tract represents a
specialization of the substantia reticularis alba and the nucleus

a similar derivative of the substantia reticularis grisea. The lemniscus (fasciculus lateralis) of these fishes represents a simi lar specialized somatic sensory path from the primary tactile and acustico-lateral centers to the nucleus lateralis mesencephali (torus semicircularis, or colliculus), whose fibers cross in the ventral commissure of the oblongata. This special splanchnic (gustatory) path appears to have been differentiated later in the phylogeny than the secondary somatic path. Hence its super- ficial position, coenogenetic structures of the brain being gen- erally added external to palingenetic structures. The crossing of the visceral path within its terminal nucleus instead of at its origin in the oblongata is perhaps due to the same cause, the primitive undifferentiated visceral path having been uncrossed or diffusely crossed because these sensations are not localized ordi- narily. The *unspecialized* secondary visceral path doubtless is as primitive as the unspecialized somatic path and probably was originally a diffuse connection by short fibers in the substantia reticularis (crossed or uncrossed). But the ascending gustatory tract (specialized visceral) as a well defined conduction path is quite certainly more recent. This does not affect the conclu- sion to which we were led above that the visceral root fibers (fasciculus communis) are older than the *special* somatic centers in the tuberculum acusticum.

The topography of the oblongata suggests that upon the basis of the unspecialized centers the ascending secondary paths for the specialized systems were added in the following order,—first, the somatic sensory, or lateralis system for orien- tation and equilibrium, and, second, the gustatory. The latter is a strictly visceral system except that in some fishes impor- tant somatic secondary connections appear sporadically in cor- relation with the appearance of taste buds in the outer skin.

The mammalian homologies of the superior secondary gus- tatory nucleus cannot be determined until its relations to neigh- boring structures are much more fully known. STIEDA's origin- al designation, ''Uebergangsganglion,'' apparently included much more than the secondary gustatory center, which is prob- ably coextensive with MAYSER's narrower term, ''Rindenkno t-

en." MAYSER ('82, p. 334) identifies the "Uebergangsgang-
lion" with the corpus quadrigeminum posterius of FRITSCH
('78). From the latter's figures, I infer that he included under
this term the structures adjacent to the secondary gustatory nu-
cleus as far as cephalad as my nucleus lateralis valvulae. The
latter nucleus is apparently included in the "cells of the super-
ior and internal regions of the torus semicircularis" of CATOIS
('01, p. 133). CATOIS' "cells of the external region of the tor-
us" constitute the nucleus lateralis mesencephali of EDINGER.
EDINGER states that the "Uebergangsganglion" of STIEDA
(sekundäre Vaguskern) is homologous with his ganglion isthmi
('96, p. 94 and '03, p. 75). He also identifies ('04, p. 194) the
ganglion isthmi with the nucleus tegmenti dorsalis of VON GUD-
DEN and thinks it probably is the same as BECHTEREW's corpus
parabigeminum. EDINGER adds ('04, p. 267) that the ganglion
isthmi of lower vertebrates receives the median root of the op-
tic nerve and gives rise to centrifugal fibers for the retina. His
account make it probable that his ganglion isthmi sould be iden-
tified with my nucleus lateralis valvulae rather than with the
"Uebergangsganglion" as a whole. Though I have not traced the
fibers of the mesial optic root so far caudad as this, yet the
connection with the post-optic commissure, referred to by
EDINGER, is very plain, and the tract running from the cephalic
end of the n. lateralis valvulae to the oculomotor nuclei lends
probability to the belief that the n. lateralis valvulae is in part
a path for oculo-motor reflexes and probably also somatic mo-
tor reflexes via the fasciculus longtitudinalis, of optic, gustatory
and perhaps olfactory origin. My n. lateralis valvulae is appar-
ently included in the "ganglio subcerebelloso" described ('94,
p. 96) and figured ('94 a, Fig. 4, p. 203) by CAJAL. His fig-
ure shows the cells provided with a single thick unbranched
dendrite which comes into relation with collaterals from the
ventral longitudinal tracts of the mid-brain.

The only conclusion at present possible is that the "Ue-
bergangsganglion" is a very complex structure, devoted large-
ly to gustatory reflexes and coordinations of several sorts, and

doubtless with other important connections as yet imperfectly known.

While these pages are passing through the press the excellent paper by GOLDSTEIN (Untersuchungen über das Vorderhirn und Zwischenhirn einiger Knochenfische, nebst einigen Beiträgen über Mittlehirn und Kleinhirn derselben. *Arch. f. mikr. Anat.*, LXVI, 2, 1905, pp. 135-220), on the brains of teleosts has come to hand. While GOLDSTEIN's detailed examination did not extend back into the region of the gustatory centers, yet I am pleased to note that he found and figured the tertiary path to the inferior lobes, though naturally without being able to give its functional interpretation. It has been assumed by some authors that the ganglion isthmi of EDINGER is the same as the "Rinden-knoten" of MAYSER (my nucleus gustus secundus superior). GOLDSTEIN, how-ever, terms the latter "nucleus lateralis cerebelli" and the cells which he desig-nates as ganglion isthmi are clearly shown by his figures to be the cortical layer of tertiary gustatory neurones surroung the "Rindenknoten" as I have describ-ed them in the preceding pages. GOLDSTEIN's tractus isthmo-hypothalamicus, then, is my tertiary gustatory path to the inferior lobe. It is apparently another portion of this tertiary gustatory path which he shows in text-figure 21 (p. 206) entering the tr. cerebello-thalami from the dorsal part of the nucleus lateralis cer-ebelli.

There remain to be considered the *morphological relations of the gustatory system* as a whole to the other functional sys-tems of the brain. The intimate association of gustatory fibers with those of general visceral sensation, both in the peripheral and the central nervous system, strongly suggests that the gus-tatory system has been specialized from this primitive source ; but it must be admitted that the evidence thus far produced, while very suggestive, can hardly be called demonstra-tive. A comparison of the gustatory system with the "viscer-al sensory system" cannot be expected to yield very impor-tant results so long as the latter system remains so imperfectly understood. There is a strong demand for an analysis of the visceral nerves and for a clear understanding of the relations (both anatomical and physiological) of their various kinds with certain systems commonly classified with the somatic sensory group, such as the nerves of muscle and joint, thermal and pain (?) sensations.

Whatever the phylogenetic origin of the gustatory system, it is clear that it is confined to the cranial nerves and that in the lowliest vertebrates it is represented in at least three of these nerves. The primary terminal center does not corres-

pond topographically with the dorsal horn of the spinal cord, but with the region of CLARKE's column. In the present state of our knowledge, no precise comparisons are possible between the gustatory secondary connections and those of the visceral centers of the spinal cord. And in the brain, where our knowledge of the connections of the nerves is more exact, there is no close resemblance between the secondary gustatory and any other secondary sensory system.

The acustico-lateral and tactile systems have been shown to be intimately related and their secondary tracts in fishes are, in a general way at least, known, crossing immediately in the ventral commissure and ascending in the lemniscus (fasciculus lateralis) to the opposite mesencephalon. Clearly there is no close resemblance here with the gustatory connections and it is difficult to conceive how either form could have been derived from the other.

Given a primitive elongated gustatory center in the oblongata, like that associated with the fasciculus communis of the amphibia, and the development of all types of primary gustatory centers known among fishes can be easily understood by simple hypertrophy of different parts of the system. We have seen in the preceding descriptions that the secondary gustatory connections are in almost all cases through the substantia reticularis grisea or derivatives from it. This applies both to the short connections and to those by way of the superior and inferior secondary nuclei. In the two latter cases the connection is partly on the same side and partly on the opposite side through a commissure.

The superior secondary nucleus is clearly adapted to serve the higher gustatory reflexes, and various coordinations, chiefly with smell and sight. The connection with the valvula cerebelli and cerebellum is very perplexing. There is a suggestion in certain comparative anatomical facts that the valvula cerebelli of teleosts (or at least its lateral lobes which are broadly confluent with the nucleus lateralis) has been differentiated in connection with the secondary gustatory nucleus. The valvula is largest in those teleosts which have the most highly developed

gustatory systems, and it was noticed by MAYSER ('82, p. 325) that the cephalic part of the "Uebergangsganglion" (including my nucleus lateralis valvulae) varies in size with the valvula cerebelli, while the caudal part (which corresponds in part with our substantia reticularis grisea trigemini) varies with the size of the secondary gustatory tracts. In Mormyrus, where the lateral lobes of the valvula attain so enormous size as to expand upwards and laterally in mushroom shape and overlap the whole brain, SANDERS ('83) describes also a considerably enlarged and modified tuberculum impar and vagal lobes. Since the other parts of this brain are of the typical teleostean type, save for the reduction of the visual apparatus and inferior lobes, it appears probable that the lateral lobes of the valvula are related with the gustatory reflexes.

The chief connections of the cerebellum are with centers commonly regarded as of the somatic sensory type—tactile, acustico-lateral, visual. This strengthens the current view that this organ is concerned with the regulation of somatic movements, or reactions of the body to external stimuli as distinguished from visceral reactions to internal stimuli. A gustatory cerebellar connection would seem, therefore, very anomalous. And so it would be in an ordinary vertebrate, if our present functional analysis is proceeding along true lines. But we have seen above that the fishes here under consideration, unlike most other vertebrates, make somatic movements in response to cutaneous gustatory stimulation in their ordinary feeding reactions. This feature gives an abundant explanation for the cerebellar connections of the secondary gustatory nucleus, by way of the nucleus lateralis valvulae, as well as a possible clue to the morphology and phylogeny of the valvula.

The problem of the relation of taste and smell is of major importance from the points of view of comparative physiology, of phylogeny and of morphology. Why the single chemical sense of some invertebrates should have given rise in the vertebrates to two systems so distinct morphologically as the olfactory and gustatory apparatus has not been explained. A suggestion of a possible genetic connection is manifest in the ac-

companying diagram (Fig. 40) of the morphological relations.

Remembering that the secondary gustatory connections are differentiations from the substantia reticularis grisea (the anomalous position of the superior secondary nucleus being easily explained on mechanical grounds), we find here a natural explanation of the further (tertiary) path to the inferior lobe, for this is also a derivative of the substantia reticularis, crowded for mechanical reasons in the opposite direction from that taken by the secondary gustatory nucleus (cf. JOHNSTON '02 a, p. 100). Turning now to the secondary olfactory connections, the resemblance to those of the sense of taste is striking in fundamentals, in spite of great difference in detail.

Fig. 40. Diagram showing the relations of the gustatory and olfactory centers in teleosts, as represented by the shaded areas. The black spots represent the position of commissures of secondary or tertiary fibers. 2, 3 and 4 represent the olfactory conduction paths of the second, third and fourth orders respectively. II, III, IV represent the gustatory conduction paths of the second, third and fourth orders respectively. Compare Figs. 38 and 39.

The olfactory bulb, like the vagal lobe, contains a marginal zone of large secondary cells, the mitral cells, with long neurites and with dendrites which receive the endings of the peripheral neurones. The interior of the bulb is filled with minute intrinsic neurones. The secondary center is the area olfactoria of the fore-brain, whose commissure bears the same relation to the secondary tracts as do those of the secondary gustatory nuclei. The main tertiary tract passes, as before, to the inferior lobe, which is, in fishes, the central correlation station for all sensory impressions. The return path from the inferior lobe to

the epistriatum in teleosts is a prophesy of the evolution of the cortex cerebri in the later phylogeny. The olfactory and gustatory tertiary tracts end together throughout the inferior lobe and they have a common descending conduction path, the tractus lobo-bulbaris. In addition to this ventral olfactory path, there is the dorsal tertiary tract from the fore-brain to the habenula and its descending path of the fourth order, MEYNERT's fasciculus retroflexus. This path offers opportunity for somatic sensory (including optic) and somatic motor connections analogous to those provided for the sense of taste in the inferior secondary nucleus.

If the olfacto-gustatory connections of the human body are at all similar to these of fishes, this relation offers a possible anatomical correlate of the familiar fact of experience that subjectively we distriminate tastes and smells only imperfectly, in many cases not at all, without the aid of collateral physiological experimentation to determine which organ receives the stimulus.

It is freely granted that these comparisons are, in the present state of our knowledge, rather fanciful. They are offered merely as the first practicable working hypothesis for a correlation of the olfactory with the other sensory mechanisms. If the anterior end of the primary nerve tube lies in the region of the preoptic recess, as seems to be now commonly assumed, the peculiar relations of the rhinencephalon are to be explained as due to the suppression of the most anterior sensory and motor centers of other systems, leaving the olfactory apparatus free to develop without constraint.

The most striking difference noticeable in the diagram between the centers for taste and smell is the apparently ventral position of the primary and secondary olfactory centers as contrasted with the dorsal centers for taste. But if the anterior end of the brain tube lies near the preoptic recess in the lamina terminalis, this difficulty disappears; for all structures in front of this point must have been developed from the dorsal wall of the brain tube. That is, the secondary fore-brain, including the entire rhinencephalon, is a dorsal structure.

Our conclusion, then, is that the morphological relations

ed, retained its superficial position with reference to them. In passing from the fishes to the mammals the fasciculus solitarius has been crowded again somewhat laterally on account of the further development of median structures.

The short gustatory paths between the primary centers and the motor nuclei of the oblongata by way of the substantia reticularis are essentially the same in the fishes and mammals.

The homology of the nucleus ambiguus of fishes and mammals is not open to question. FOREL in 1891 showed that the so-called chief or dorsal sensory nucleus of the IX and X nerves of mammals is in reality a motor nucleus of origin for these nerves and much evidence in confirmation of this view has since been published. The motor layer of the vagal lobe of cyprinoids corresponds in position exactly with this nucleus and is probably in a broad way homologous with it, though of course the homology is not exact.

The long ascending secondary tracts from the vagal and facial lobes (central gustatory path, or tractus secundus ascendens) has not been identfied in any vertebrates save the fishes, though it has long been in the minds of several neurologists that the homologies of this tract are to be sought in the lateral cerebellar tract of FLECHSIG (tractus spino-cerebellaris dorsalis, EDINGER). These fibers are known to arise from the cells of CLARKE'S column (supposed to be a visceral sensory center) and to enter the vermis cerebelli by way of the restiform body of the same side. Dorsally of the ventricle they cross to the opposite side and the whole arrangement strongly suggests a survival of a primitive secondary tract from the visceral sensory center of the spinal cord to the isthmus, to which in fishes the strong secondary gustatory tracts arising in the oblongata are added. This suggestion, however, cannot be taken seriously until we have much more exact knowledge of the superior connections of these fibers in the mammals and of the comparative anatomy of the structures at the base of the vermis cerebelli.

The morphological relations of the secondary gustatory tract and nucleus are clearly defined. The tract represents a specialization of the substantia reticularis alba and the nucleus

a similar derivative of the substantia reticularis grisea. The lemniscus (fasciculus lateralis) of these fishes represents a simi lar specialized somatic sensory path from the primary tactile and acustico-lateral centers to the nucleus lateralis mesencephali (torus semicircularis, or colliculus), whose fibers cross in the ventral commissure of the oblongata. This special splanchnic (gustatory) path appears to have been differentiated later in the phylogeny than the secondary somatic path. Hence its superficial position, coenogenetic structures of the brain being generally added external to palingenetic structures. The crossing of the visceral path within its terminal nucleus instead of at its origin in the oblongata is perhaps due to the same cause, the primitive undifferentiated visceral path having been uncrossed or diffusely crossed because these sensations are not localized ordinarily. The *unspecialized* secondary visceral path doubtless is as primitive as the unspecialized somatic path and probably was originally a diffuse connection by short fibers in the substantia reticularis (crossed or uncrossed). But the ascending gustatory tract (specialized visceral) as a well defined conduction path is quite certainly more recent. This does not affect the conclusion to which we were led above that the visceral root fibers (fasciculus communis) are older than the *special* somatic centers in the tuberculum acusticum.

The topography of the oblongata suggests that upon the basis of the unspecialized centers the ascending secondary paths for the specialized systems were added in the following order,—first, the somatic sensory, or lateralis system for orientation and equilibrium, and, second, the gustatory. The latter is a strictly visceral system except that in some fishes important somatic secondary connections appear sporadically in correlation with the appearance of taste buds in the outer skin.

The mammalian homologies of the superior secondary gustatory nucleus cannot be determined until its relations to neighboring structures are much more fully known. STIEDA's original designation, "Uebergangsganglion," apparently included much more than the secondary gustatory center, which is probably coextensive with MAYSER's narrower term, "Rindenknot-

en." MAYSER ('82, p. 334) identifies the "Uebergangsgang-
lion" with the corpus quadrigeminum posterius of FRITSCH
('78). From the latter's figures, I infer that he included under
this term the structures adjacent to the secondary gustatory nu-
cleus as far as cephalad as my nucleus lateralis valvulae. The
latter nucleus is apparently included in the "cells of the super-
ior and internal regions of the torus semicircularis" of CATOIS
('01, p. 133). CATOIS' "cells of the external region of the tor-
us" constitute the nucleus lateralis mesencephali of EDINGER.
EDINGER states that the "Uebergangsganglion" of STIEDA
(sekundäre Vaguskern) is homologous with his ganglion isthmi
('96, p. 94 and '03, p. 75). He also identifies ('04, p. 194) the
ganglion isthmi with the nucleus tegmenti dorsalis of VON GUD-
DEN and thinks it probably is the same as BECHTEREW'S corpus
parabigeminum. EDINGER adds ('04, p. 267) that the ganglion
isthmi of lower vertebrates receives the median root of the op-
tic nerve and gives rise to centrifugal fibers for the retina. His
account make it probable that his ganglion isthmi sould be iden-
tified with my nucleus lateralis valvulae rather than with the
"Uebergangsganglion" as a whole. Though I have not traced the
fibers of the mesial optic root so far caudad as this, yet the
connection with the post-optic commissure, referred to by
EDINGER, is very plain, and the tract running from the cephalic
end of the n. lateralis valvulae to the oculomotor nuclei lends
probability to the belief that the n. lateralis valvulae is in part
a path for oculo-motor reflexes and probably also somatic mo-
tor reflexes via the fasciculus longtitudinalis, of optic, gustatory
and perhaps olfactory origin. My n. lateralis valvulae is appar-
ently included in the "ganglio subcerebelloso" described ('94,
p. 96) and figured ('94 a, Fig. 4, p. 203) by CAJAL. His fig-
ure shows the cells provided with a single thick unbranched
dendrite which comes into relation with collaterals from the
ventral longitudinal tracts of the mid-brain.

The only conclusion at present possible is that the "Ue-
bergangsganglion" is a very complex structure, devoted large-
ly to gustatory reflexes and coordinations of several sorts, and

doubtless with other important connections as yet imperfectly known.

While these pages are passing through the press the excellent paper by GOLDSTEIN (Untersuchungen über das Vorderhirn und Zwischenhirn einiger Knochenfische, nebst einigen Beiträgen über Mittlehirn und Kleinhirn derselben. *Arch. f. mikr. Anat.*, LXVI, 2, 1905, pp. 135-220), on the brains of teleosts has come to hand. While GOLDSTEIN's detailed examination did not extend back into the region of the gustatory centers, yet I am pleased to note that he found and figured the tertiary path to the inferior lobes, though naturally without being able to give its functional interpretation. It has been assumed by some authors that the ganglion isthmi of EDINGER is the same as the "Rinden-knoten" of MAYSER (my nucleus gustus secundus superior). GOLDSTEIN, however, terms the latter "nucleus lateralis cerebelli" and the cells which he designates as ganglion isthmi are clearly shown by his figures to be the cortical layer of tertiary gustatory neurones surroung the "Rindenknoten" as I have described them in the preceding pages. GOLDSTEIN's tractus isthmo-hypothalamicus, then, is my tertiary gustatory path to the inferior lobe. It is apparently another portion of this tertiary gustatory path which he shows in text-figure 21 (p. 206) entering the tr. cerebello-thalami from the dorsal part of the nucleus lateralis cerebelli.

There remain to be considered the *morphological relations of the gustatory system* as a whole to the other functional systems of the brain. The intimate association of gustatory fibers with those of general visceral sensation, both in the peripheral and the central nervous system, strongly suggests that the gustatory system has been specialized from this primitive source ; but it must be admitted that the evidence thus far produced, while very suggestive, can hardly be called demonstrative. A comparison of the gustatory system with the "visceral sensory system" cannot be expected to yield very important results so long as the latter system remains so imperfectly understood. There is a strong demand for an analysis of the visceral nerves and for a clear understanding of the relations (both anatomical and physiological) of their various kinds with certain systems commonly classified with the somatic sensory group, such as the nerves of muscle and joint, thermal and pain (?) sensations.

Whatever the phylogenetic origin of the gustatory system, it is clear that it is confined to the cranial nerves and that in the lowliest vertebrates it is represented in at least three of these nerves. The primary terminal center does not corres-

pond topographically with the dorsal horn of the spinal cord, but with the region of CLARKE's column. In the present state of our knowledge, no precise comparisons are possible between the gustatory secondary connections and those of the visceral centers of the spinal cord. And in the brain, where our knowledge of the connections of the nerves is more exact, there is no close resemblance between the secondary gustatory and any other secondary sensory system.

The acustico-lateral and tactile systems have been shown to be intimately related and their secondary tracts in fishes are, in a general way at least, known, crossing immediately in the ventral commissure and ascending in the lemniscus (fasciculus lateralis) to the opposite mesencephalon. Clearly there is no close resemblance here with the gustatory connections and it is difficult to conceive how either form could have been derived from the other.

Given a primitive elongated gustatory center in the oblongata, like that associated with the fasciculus communis of the amphibia, and the development of all types of primary gustatory centers known among fishes can be easily understood by simple hypertrophy of different parts of the system. We have seen in the preceding descriptions that the secondary gustatory connections are in almost all cases through the substantia reticularis grisea or derivatives from it. This applies both to the short connections and to those by way of the superior and inferior secondary nuclei. In the two latter cases the connection is partly on the same side and partly on the opposite side through a commissure.

The superior secondary nucleus is clearly adapted to serve the higher gustatory reflexes, and various coordinations, chiefly with smell and sight. The connection with the valvula cerebelli and cerebellum is very perplexing. There is a suggestion in certain comparative anatomical facts that the valvula cerebelli of teleosts (or at least its lateral lobes which are broadly confluent with the nucleus lateralis) has been differentiated in connection with the secondary gustatory nucleus. The valvula is largest in those teleosts which have the most highly developed

gustatory systems, and it was noticed by MAYSER ('82, p. 325) that the cephalic part of the "Uebergangsganglion" (including my nucleus lateralis valvulae) varies in size with the valvula cerebelli, while the caudal part (which corresponds in part with our substantia reticularis grisea trigemini) varies with the size of the secondary gustatory tracts. In Mormyrus, where the lateral lobes of the valvula attain so enormous size as to expand upwards and laterally in mushroom shape and overlap the whole brain, SANDERS ('83) describes also a considerably enlarged and modified tuberculum impar and vagal lobes. Since the other parts of this brain are of the typical teleostean type, save for the reduction of the visual apparatus and inferior lobes, it appears probable that the lateral lobes of the valvula are related with the gustatory reflexes.

The chief connections of the cerebellum are with centers commonly regarded as of the somatic sensory type—tactile, acustico-lateral, visual. This strengthens the current view that this organ is concerned with the regulation of somatic movements, or reactions of the body to external stimuli as distinguished from visceral reactions to internal stimuli. A gustatory cerebellar connection would seem, therefore, very anomalous. And so it would be in an ordinary vertebrate, if our present functional analysis is proceeding along true lines. But we have seen above that the fishes here under consideration, unlike most other vertebrates, make somatic movements in response to cutaneous gustatory stimulation in their ordinary feeding reactions. This feature gives an abundant explanation for the cerebellar connections of the secondary gustatory nucleus, by way of the nucleus lateralis valvulae, as well as a possible clue to the morphology and phylogeny of the valvula.

The problem of the relation of taste and smell is of major importance from the points of view of comparative physiology, of phylogeny and of morphology. Why the single chemical sense of some invertebrates should have given rise in the vertebrates to two systems so distinct morphologically as the olfactory and gustatory apparatus has not been explained. A suggestion of a possible genetic connection is manifest in the ac-

companying diagram (Fig. 40) of the morphological relations.

Remembering that the secondary gustatory connections are differentiations from the substantia reticularis grisea (the anomalous position of the superior secondary nucleus being easily explained on mechanical grounds), we find here a natural explanation of the further (tertiary) path to the inferior lobe, for this is also a derivative of the substantia reticularis, crowded for mechanical reasons in the opposite direction from that taken by the secondary gustatory nucleus (cf. JOHNSTON '02 a, p. 100). Turning now to the secondary olfactory connections, the resemblance to those of the sense of taste is striking in fundamentals, in spite of great difference in detail.

Fig. 40. Diagram showing the relations of the gustatory and olfactory centers in teleosts, as represented by the shaded areas. The black spots represent the position of commissures of secondary or tertiary fibers. 2, 3 and 4 represent the olfactory conduction paths of the second, third and fourth orders respectively. II, III, IV represent the gustatory conduction paths of the second, third and fourth orders respectively. Compare Figs. 38 and 39.

The olfactory bulb, like the vagal lobe, contains a marginal zone of large secondary cells, the mitral cells, with long neurites and with dendrites which receive the endings of the peripheral neurones. The interior of the bulb is filled with minute intrinsic neurones. The secondary center is the area olfactoria of the fore-brain, whose commissure bears the same relation to the secondary tracts as do those of the secondary gustatory nuclei. The main tertiary tract passes, as before, to the inferior lobe, which is, in fishes, the central correlation station for all sensory impressions. The return path from the inferior lobe to

the epistriatum in teleosts is a prophesy of the evolution of the cortex cerebri in the later phylogeny. The olfactory and gustatory tertiary tracts end together throughout the inferior lobe and they have a common descending conduction path, the tractus lobo-bulbaris. In addition to this ventral olfactory path, there is the dorsal tertiary tract from the fore-brain to the habenula and its descending path of the fourth order, MEYNERT's fasciculus retroflexus. This path offers opportunity for somatic sensory (including optic) and somatic motor connections analogous to those provided for the sense of taste in the inferior secondary nucleus.

If the olfacto-gustatory connections of the human body are at all similar to these of fishes, this relation offers a possible anatomical correlate of the familiar fact of experience that subjectively we distriminate tastes and smells only imperfectly, in many cases not at all, without the aid of collateral physiological experimentation to determine which organ receives the stimulus.

It is freely granted that these comparisons are, in the present state of our knowledge, rather fanciful. They are offered merely as the first practicable working hypothesis for a correlation of the olfactory with the other sensory mechanisms. If the anterior end of the primary nerve tube lies in the region of the preoptic recess, as seems to be now commonly assumed, the peculiar relations of the rhinencephalon are to be explained as due to the suppression of the most anterior sensory and motor centers of other systems, leaving the olfactory apparatus free to develop without constraint.

The most striking difference noticeable in the diagram between the centers for taste and smell is the apparently ventral position of the primary and secondary olfactory centers as contrasted with the dorsal centers for taste. But if the anterior end of the brain tube lies near the preoptic recess in the lamina terminalis, this difficulty disappears ; for all structures in front of this point must have been developed from the dorsal wall of the brain tube. That is, the secondary fore-brain, including the entire rhinencephalon, is a dorsal structure.

Our conclusion, then, is that the morphological relations

expressed in Fig. 40 strongly suggest that the central reflex mechanisms of taste and smell have had a common phylogenetic origin and that they have been from the first quite independent of the so-called somatic sensory centers.

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brates, with its Relation to the Decussation of the Optic Nerves, the Ocu-
lar Movements, and the Pupil Light Reflex. *Brain*, 1904, **27.** 107-147.

'Stereoscopic' vision differs from 'binocular' in that in the former
the images of a given object fall simultaneously on homonymous sides
of the two retinae, while in the latter they may fall either homonymous-
ly or heteronymously. Now from examining experimentally the optic
chiasm in the toad, chameleon, pigeon, owl, and rabbit, and from the
reports of others on the cat, mouse and rat, the author concludes (p.
107) that "The decussation of the optic nerves at the chiasma is com-
plete in all fishes, amphibia, reptiles and birds, whether possessed of
binocular vision or not;" and this notwithstanding that (p. 111) "In
the lowest fishes, the cyclostoma, ... the optic nerves do not cross
the middle line, but each arises from the corresponding side of the fore-
brain, the nerves passing to the eyes without decussation." At most,
the author may be said to have shown that 'binocular' (but not stereo-
scopic) vision is not incompatible with total decussation at the chiasm.
He thinks probable that "the association of the visual impression re-
ceived by the two eyes of the same object is effected by the commissur-
al fibres of the corpus callosum." True stereoscopic vision is suppos-
ed impossible unless the decussation is only partial, that is, unless the
optic fibres from homonymous sides of the retinae lead to the same
cortical centres.

The macula lutea is probably not represented in both halves of
the brain as has sometimes been concluded from the fact that in most
cases of permanent hemianopia, the dividing line between the blind
and the seeing halves of the field is found to pass around the fixation
point, leaving it included in the seeing half of the field for each eye.
But this fact is probably due to a greater power of resisting disease
possessed by the macular fibres, since in cases of transient hemianopia
the dividing line between the seeing and the blind fields passes exact-
ly through the fixation point, and when recovery sets in it begins at the
macular region. The macular fibres do not bifurcate at the chiasm.

Conjugate, lateral and vertical movements of the two eyes (but
not movements of convergence) are directly associated with semi-
decussation of the optic nerves at the chiasm. The more complete

the decussation, the more independently of each other the eyes will be apt to move.

As to the pupillary reflex, Dr. HARRIS finds (p. 139) that "in all those animals in which there is a total decussation of the optic nerves at the chiasma, only that pupil contracts which is exposed to light." In such animals the course of the reflex is probably from the eye along the optic nerve and tract to the anterior corpus quadrigeminum of the opposite side, thence by MEYNERT'S fountain decussation to the nucleus of the third nerve on the former side, and thence back by the third nerve to the iris of the eye stimulated. In man and higher animals where the pupillary reflex to stimulation of one eye is binocular (consensual), the anterior corpus quadrigeminum of either side must be connected with the third nerve nuclei on both sides.   E. B. H.

Le Bon, Gustave. Psychologie de l'Education. *Paris, Flammarion,* 1904. (5. éd.) pp. 304.

LE BON'S discussion of the psychological bases of teaching is of interest to comparative psychologists, for he maintains that instincts develop from conscious acts From this point of view all developmental progress in the race, as in the individual, is conditioned by the mechanizing of conscious activities. Education itself should be, in LE BON'S opinion, the facilitation of this process. "L'éducation est l'art de faire passer le conscient dans l'inconscient."

LE BON'S treatment of the psychology of instruction and education makes clear the significance of studies in the development of activity, and suggests to the comparative psychologist certain lines of investigation which may yield results of practical importance in education.   R. M. Y.

E. Bolnet. Les Doctrines Médicales, Leur Evolution. Bibliothéque de Philosophie scientifique, *Flammarion, Editeur, Paris, 1905.*

A brief account of medical doctrines from the time antedating HIPPOCRATES, through the Middle Ages, to PASTEUR. The modern theories of immunity and of infection, with their applications to therapy and hygiene, are discussed.   W. B. C.

J. Hericonot. Les Frontièrs de la Maladie. Bibliothèque de Philosophie Scientifique, *Flammarion, Editeur, Paris, 1905.*

An interesting and important discussion of the borderland between health and disease. The insideous beginnings of disturbances of nutrition and metabolism, of auto-intoxication, of chronic infectious diseases, and of attenuated forms of acute infections are treated in an illuminating manner.   W. B. C.

SOME CELLULAR CHANGES IN THE PRIMARY OPTIC VESICLES OF NECTURUS.

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With Plate V.

A superficial study of the optic vesicles as they develop in Necturus showed certain interesting features, which have not been heretofore described. On account of the large size of its cellular elements, the cytological changes in this animal admit of a more exact interpretation than is afforded by other vertebrates.

The formation of the neural plate in Necturus is initiated by certain changes in the ectodermal cells, which elongate from the low cuboidal of the superficial ectoderm to the long columnar type, as shown in Fig. 1, *e.c* and *n.c.* The same changes are shown under higher magnification in Figs. 7 and 8, Fig. 7 representing a cell near the center of the neural plate, and Fig. 8 an ectodermal cell beyond the margin of the neural plate.

The cells of which Fig. 7 is a type are divisible into two parts, a proximal and a distal. The former is full of yolk granules and usually contains the nucleus. This nucleus varies in shape from round to long oval, its long diameter being from two to three times the short. Sometimes it is irregular in shape, in which case it is usually found near the center of the neural plate. When the nucleus lies in the distal part of the cell, it is frequently observed undergoing mitosis.

The distal part of the cell may contain a few yolk granules, which are usually small and of indistinct contour, as shown in Fig. 7. This portion does not stain readily, shows a distinct membrane, and is free from yolk granules. Such polarity is most marked in the cells (Fig. 1, *n c.*) near the center of the neural plate. From here outwards, towards either side of the neural plate, the nuclei are rounder, the cells shorter, and the granules encroach more and more on the clear portion of the cell.

As soon as the neural plate is well defined (Fig. 2, *n.p.*), the outlines of the individual cells become less distinct, though each presents the same general characteristics observed in the preceding stage, as represented in Fig. 7. The neural plate is now composed of two or three layers of columnar cells. The neural cells forming the upper layer show the portion spoken of above as free from yolk granules. They are so arranged that a clear band stretches from one margin of the plate to the other. The ectoderm of the remainder of the embryo becomes two-layered as it approaches the neural plate, and ends abruptly at the margins of the latter, which already shows an incipient infolding (Fig. 2, *n.p.*). The further development of the neural plate is characterized by an increase in the number of cells composing it, and by an approximation of its margins, which grow together to form a tube, as shown in Figs. 3, 4 and 5.

By the time the anterior part of the neural canal is formed and the *Anlagen* of the optic vesicles appear, the neural tube has the general shape of a spherical triangle, the two basal angles being formed by the *Anlagen* of the optic vesicles (Fig. 3, *o.v.*). The plane of the section represented is through a part where the canal has not quite closed. The wall is composed of many layers of cells, and varies in thickness in different localities. It is, in general, thinner in the region of the future optic vesicles. The cells forming the lining layer abut upon the lumen in an irregular line, as represented in Fig. 3.

The nuclei (*n.n.*) in the wall of the neural canal vary greatly in outline. Some are round, some oblong, while a large

number are irregular, showing a prolongation in the direction
of the lumen. Some of the latter are shown under higher mag-
nification, in Figs. 9, 10, 11. These represent three cells from
the same field, and illustrate different stages of the same phe-
nomenon. The body of each nucleus shows a number of scat-
tered karyosomes, while the prolongation is more or less striat-
ed, the striae running parallel to its long axis. The appearance
of the cytoplasm and the nuclei indicates that the cells are
migratory.

Some of the nuclei are undergoing karyokinesis and these,
as well as the ameboid forms of nuclei, are more numerous
where the walls are thinnest, being especially so in the region
of the optic vesicles. In places the cells are seen dividing,
where one-half is being thrust out into the lumen.

The lumen of the canal contains a mass which can be re-
solved into three constituents; (1) and most numerous, are round
structures slightly larger than the neighboring nuclei, which are
massed together and more or less completely fill the lumen.
These will be shown to be cells in various stages of degenera-
tion ; (2) nuclei and larger remnants of the same ; (3) detritus.

The first of the contents of the lumen consists of well de-
fined cell outlines. They are round, of nearly constant size,
having an average diameter of 40 μ, and are usually clear and
devoid of yolk granules, as depicted in Fig. 3, *l.c*, They are
more numerous near the head end of the embryo, especially in
the region of the future optic vesicles.

The nuclei lying in the lumen are, in a varying degree, small-
er and less deeply stained than those in the wall of the tube.
They may be round or may assume ameboid forms (Figs. 12,
13, 14). Some are pear shaped (Figs. 13, 14), with the larger
mass extending into the lumen. Many appear (Fig. 13) as if
the chromatin is passing out of the basal portion of the cell and
becoming rounded up in the distal portion.

The round forms of the nuclei either show a cell membrane
around them, or where this is not distinct, there are yolk gran-
ules present, indicating the position of the cell. A few nuclei
lie in the lumen independent of any connections with a cell, but

from their small size, faint staining capacity, and general indistinctness, we may conclude that they are degenerating.

The third constituent of the contents of the lumen is a debris composed of fragments of yolk granules, disintegrating nuclei, and remains of cell membranes.

In the next stage (Fig. 4) the development of the embryo has advanced so far that the optic vesicles (*o.v.*) are distinct evaginations of the neural canal. The figure shows a section through the neural canal and the centers of the optic vesicles. The nuclei of the neural cells lying next to the lumen show a tendency to assume ameboid forms which however, are not as pronounced as in the preceding stage. They are most numerous in the dorsal wall of the canal, and in the superior wall of the optic vesicles. Along the margin, nuclei undergoing degeneration are occasionally seen.

The center of the lumen is entirely free from cellular elements or their remnants. The remainder of the neural canal shows the cell outlines described above, some nuclei and a few yolk granules. The cells of the optic vesicles are more compact, larger and more irregular than those lying towards the center of the canal. Where the section does not pass exactly through the center of the optic vesicles, but on either side, the central space is larger, and the mass of cell outlines lies in or near the optic vesicles. The nuclei lying in the lumen are round and no longer show ameboid forms. In Fig. 4, there are shown nuclei (*l.n.*) with well defined chromatin threads, while in other nuclei these threads have fused into a dense mass.

Fig. 5 represents a section through the neural canal and optic vesicles (*o.v.*) of the next stage. The cells in the wall are arranged in two or three layers. The dorsal wall of the canal is still from three to six layers of cells in thickness, but most of the nuclei are ameboid in shape or undergoing mitosis. In the lumen the conditions described above are accentuated. The clear central space is very large and extends nearly from the dorsal to the ventral wall of the canal. The remainder of the lumen, especially the optic vesicles, is filled with cells and nuclei in various stages of degeneration.

In the next stage (Fig. 6, *o.v.*), the optic vesicles are join-ed to the neural canal by a short hollow stalk. The nuclei lying in the wall of both the neural tube and the optic vesicles (*n.n.*) are oval or round, there being no ameboid forms present. By this time, the cellular elements have disappeared from the cavities of both the neural canal and the optic vesicles. A minimal amount of detritus can be detected, but this is proba-bly of accidental origin; at any rate it bears no resemblance to what has been described and depicted in the earlier stages. During the later development of the embryo, the lumen re-mains clear until it is obliterated by the approximation of the outer and inner layers of the optic cup.

Of special interest are; (a) the nature, (b) the origin, and (c) the fate of the structures found in the neural canal and optic vesicles. While these questions cannot be answered to com-plete satisfaction, enough is known to show that they are prob-ably of great significance

In regard to their nature, there is hardly any doubt that they are cells. They have the form and physical properties of cells, some possess a nucleus, and many contain yolk granules. They are too numerous to be accidental, and too regular and characteristic to be the product of coagulated albumin. Their number, regularity, and position, coupled with the general appearance of the sections, speak against the assumption that they are portions of long columnar cells cut obliquely. Taking all these facts into consideration, it is probably correct to regard them as cells which in some way have passed into the lumen of the canal.

As to the origin of the cells, it would seem that they are derived from the cells in the wall of the neural canal, including the optic vesicles, in one of two ways; (a) by a migration of a part or all of the cell into the lumen of the canal, and (b) by a mitosis of the cells lining the canal, with extrusion into it of one of the daughter cells. Numerous examples of the former process are found, to a few of which reference has been made (Figs. 9, 10, 11, 12, 13, 14). Examples of (b) are more rare-ly found, but are undoubtedly present.

As to the fate of the cells, it may be said that as soon as the cell enters the canal, it becomes rounded and the nucleus undergoes chromatolysis and disintegrates, followed by the remainder of the cell, the cell membrane being the last structure to vanish. The cells most distant from the neural wall are the first to disintegrate and are in some way absorbed, leaving a clear central space. This process continues until all the cells have disappeared and the clear space is identical with the central cavity of the neural canal and the optic vesicles.

A word might be added in regard to the development of the optic vesicles in the Dipnoans (3, p. 439), the Ganoids (1, p. 365) and the Teleosts (2, p. 185 ; 5, p. 243). In these, the eye develops as a solid outgrowth from a solid neural tube, and a cavity subsequently arises either by a splitting apart of the cells, or by an actual absorption of those lying most centrally.

In the Amniota, (4), on the other hand, e. g. birds and mammals, the optic vesicles develop as hollow projections of the wall of the neural tube, whose cavities subsequently become obliterated by the approximation of their walls.

The process observed in Necturus conforms to neither type. As shown above, the walls of the optic vesicle increase rapidly in thickness until a certain maximal stage is reached, after which they undergo a thinning until practically only a single layer remains. During this period, the peculiar cells described above appear in the lumen and undergo disintegration. The wall of the optic vesicle at the time it begins to bud off from the main neural tube encloses a cavity which is filled with cast off cells from its own wall, on the way to disintegration. Once free from its contents, the vesicle proceeds to develop without again showing these structures.

It is thus seen that in its development, the eye passes through a stage that certainly recalls the condition found in so many of the Anamnia. Whether or not this is to be considered of phylogenetic significance must remain an open question for the present.

The specimens on which the preceding observations were

made are a part of the private collection of Professor A. C. EYCLESHYMER, to whom I am indebted for their use, and for valuable assistance.

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EXPLANATION OF FIGURES.

LIST OF ABBREVIATIONS.

e.c.—ectodermal cells.

l.c.—cells in lumen of neural canal.

l.n.—nuclei in lumen of neural canal.

n.—nuclei.

n.c.—cell in wall of neural plate or tube.

n.n.—nuclei in wall of neural tube.

n.p.—neural plate.

o.v.—optic vesicles.

p.—projection of nucleus.

y.c.—yolk cells.

y.g.—yolk granules.

PLATE V.

Fig. 1, represents a transverse section of a 12-day embryo of Necturus through the anterior portion of the cephalic neural plate.

Fig. 2, represents a transverse section of a 14-day embryo of Necturus through the region of the *Anlagen* of the primary optic vesicles.

Fig. 3, represents a transverse section of a 16-day embryo of Necturus through the primary optic vesicle. In this stage the neural folds have approximated, but are as yet not closed. The optic vesicles and the neural groove are filled with cellular structures.

Fig. 4, represents a transverse section of an 18-day embryo of Necturus through the primary optic vesicles, which are now well defined. The neural folds have closed, and the superficial epiblast has separated from the neural epiblast. The cellular contents of the neural canal are less compact, indicating the beginning of cell disintegration in the median portion.

Fig. 5, represents a transverse section of an 18 1-2-day embryo of Necturus passing through the primary optic vesicles, whose walls are now thinned to a single layer of cells, as shown in the optic vesicle on the right. Cellular disintegration has taken place at the center of the neural canal, leaving a well defined clear space. This condition represents an advance beyond that shown in Fig. 4.

Fig. 6, represents a section, intermediate between horizontal and transverse, of a 20-day embryo of Necturus. The optic vesicles are well advanced, showing a distinct evagination and backward growth. At this time the lumen is entirely free from cells or their remains.

Figs. 7-15, illustrate the cytologic changes in the cytoplasm and nuclei of the cells which take part in the formation of the walls and cavities of the primary optic vesicles.

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PLATE V.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10

Fig. 11

Fig. 12
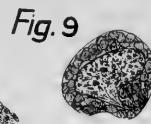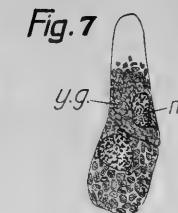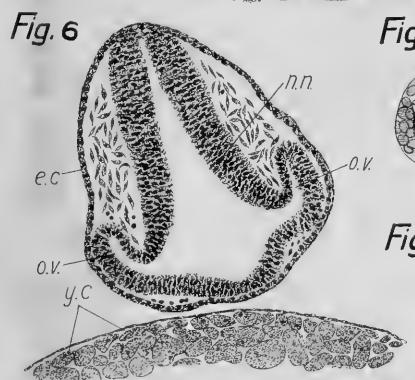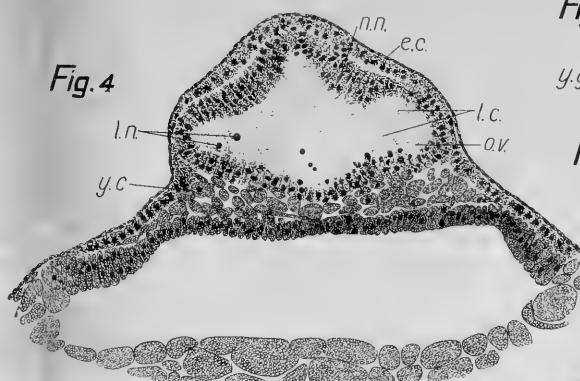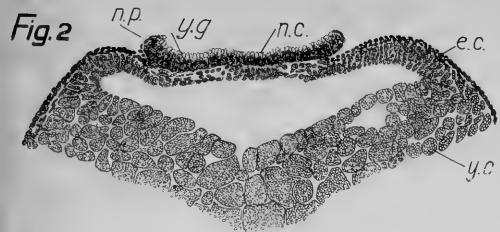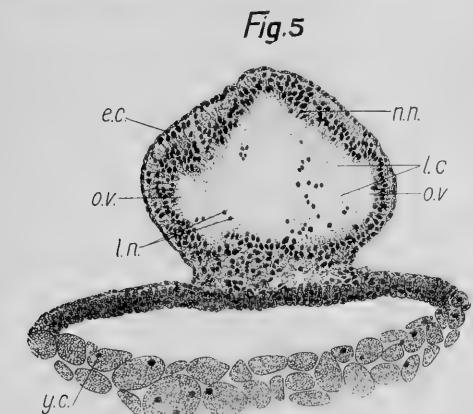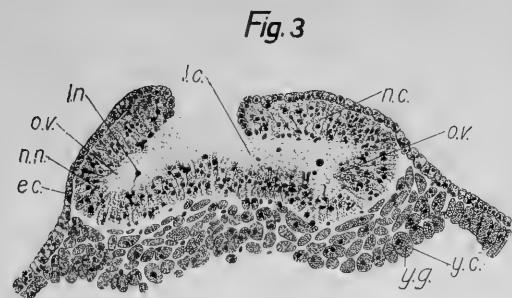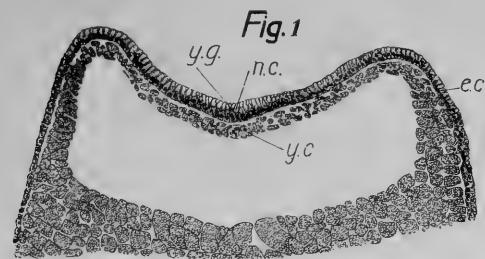
Fig. 13

Fig. 14

Fig. 15

SOME RESULTS OF A STUDY OF VARIATION AND CORRELATION IN BRAIN-WEIGHT.

By Raymond Pearl.

The purpose of this paper is to give a brief account of certain of the more general results of a quantitative study of the variation in the weight of the adult human brain, and of the correlation which exists between this and other physical characters. The investigation was undertaken with the idea that by an application of biometric methods to these problems it would be possible to reach somewhat more certain conclusions in regard to them than had previously been attained. As the work progressed its originally planned scope was considerably extended. The complete account of the results has appeared in *Biometrika*, Volume 4, No. 1. It has seemed advisable to publish a brief summary of some of the more important results and conclusions here. On account of lack of space it will be necessary in this paper to state many of the points in a somewhat categorical form without adequate discussion of the evidence on which they are based. A full presentation of the evidence must be sought in the complete paper.

1. *Material.* As material for this study the following well known series of brain-weighings were used: (1) Marchand's (:02) Hessian series, including 475 male and 281 female complete records for persons between the ages of 15 and 80; (2) Bischoff's ('80) Bavarian series, including complete records of 365 males and 241 females between the ages of 20 and 80; (3) the admirable series collected by Retzius (:00) from the Swedish population, including, after casting out incomplete records, data for 416 males and 233 females between the ages of 20 and 80; (4) Matiegka's (:03) Bohemian (Czech) series, which includes records for 372 males and 197 females. In addition to these series a portion of the Boyd-Marshall data ob-

served at the St. Marylebone Infirmary was used for a special purpose. For this last material I am indebted to Professor H. H. DONALDSON, who very kindly placed at my disposal his manuscript copy of MARSHALL'S original tables which were never published in their complete form.

An account of the methods in which the weighings were made in the different series, together with a discussion of the objections to which they are open, is given in the complete paper.

The usual biometric methods were followed in the determination of the various constants. Each series was treated separately. For reasons which need not be entered into here it appeared advisable to deal separately with two different age groupings of the material. One of these groups included all individuals falling in age between 20 (in the MARCHAND series 15) and 80. This forms what I have called the "Total" group. The other group which I have designated the "Young" group includes those individuals falling in age between 20 (in the MARCHAND series 15) and 50. It will be understood that throughout the paper "Total" and "Young" refer to these age groups.

The other characters studied besides brain-weight were stature, age, body-weight, skull length, skull breadth and the weight of the cerebrum. The units in which the constants are given are: brain-weight in grams, stature in centimetres, body-weight in kilograms, skull length and skull breadth in millimetres and weight of cerebrum in grams.

2. *Brain-weight Types.* A study of the means and their probable errors shows that there are definite racial types in this character. The differences between different races in respect to weight of brain are only in part to be accounted for by differences in other characters of the body. Two of the races studied (Swedish and Hessian) are sensibly alike in mean brain-weight. These are the two races out of the four studied which on other grounds are thought to be most closely related ethnically (cf. on this point RIPLEY ('99) and DENIKER (:00)). That differences in mean brain-weight in different races are not to be

accounted for solely by differences in other characters is shown in the following table.

TABLE I.

			Probable Brain-weight of a group of Hessians of the same *sex age* and *stature* as the	Mean Brain-weight *ob-served.* (Bavarian or Bo-hemian)	Difference expressed as in ex-cess or de-fect of Hessian values.	Difference as percent of observ-ed mean. (Bavarian or Bo-hemian)	Equation on which Hessian estimate is based.
Bavarian	♂ ♂	(Total)	1388.984	1363.185	—25.799	—1.9%	No. 23.
"	♀ ♀	(Total)	1265.137	1220.356	—44.781	—3.7%	" 25.
"	♂ ♂	(Young)	1397.157[1]	1369.110	—28.047	—2.0%	" 24.
"	♀ ♀	(Young)	1277.317[1]	1235.504	—41.813	—3.4%	" 26.
Bohemian	♂ ♂	(Total)	1394.570[2]	1454.839	+60.269	+4.1%	" 23.
"	♀ ♀	(Total)	1259.310[2]	1310.914	+51.604	+3.9%	" 25.
"	♂ ♂	(Young)	1399.527[3]	1460.150	+60.623	+4.2%	" 24.
"	♀ ♀	(Young)	1278.935[3]	1313.910	+34.975	+2.7%	" 26.

[1] This assumes that the mean stature of the Bavarians would be the same in the "young" as it is in the "total" group. The error introduced by this procedure is practically negligible.

[2] Here again, on account of lack of data, the mean stature is assumed to be the same in "total" and "young" groups.

[3] The mean age for the Bohemian "young" series was calculated by taking the first four age classes of the "total" series. The age as given is probably a little too high, but the error cannot be great. See complete paper on this point.

The values in the first column of this table were obtained by the use of the indicated characteristic equations given farther on in this paper (p. 478). Each of these represents the probable mean brain-weight (in grams) of an array of the specified type in respect to the other characters, sex, age, and stature. It shows, in other words, what would be the effect on brain-weight of se-lecting a group of Hessians of either sex to the age and stature type shown by the adult Bohemian or Bavarian population with which we are dealing. The table shows that even after Hessians, Bavarians, and Bohemians are put on the same basis with reference to sex, age and stature they still exhibit consid-erable differences in the weight of the brain.

3. *Variation in Brain-weight.* In degree of variability the characters brain-weight and skull capacity are sensibly equal. The coefficients of variation for brain-weight (and skull capaci-ty) are intermediate in value between those which have been

determined for skeletal characters in man on the one hand, and those for the weights of the viscera and various physiological characters on the other hand. The values of the standard deviations (in grams) and the coefficients of variation (in per cent.) for the different series are shown in Table II.

TABLE II.

Comparison of Different Races in Respect to Variation in Brain-weight and Skull Capacity.

Males.			Females.		
	S. D.	C.of V		S. D.	C.of V.
Swedes	106.329	7.592	Bohemians	96.772	7.382
Bohemians	113.608	7.809	Swedes	100.757	8.043
Hessians	112.675	8.096	Hessians	102.368	8.125
Bavarians	110.666	8.118	Bavrians	101.776	8.340
English[1]	124.48	9.20	English[1]	118.7	9.72
Skull Capacity–English[2]	____.__	8.28	Skull capacity–English[2]	____.__	8.68
" " –Germans[3]	____.__	7.74	" " –Germans[3]	____.__	8.19

[1]Pearson, '97, p. 321.　　[2]W. R. Macdonell, :04, p. 221.
[3]Pearson, '97, p. 333.

The values of the probable errors of these constants are such as to show that the differences in variability between the different races are not significant, but merely such as might arise from random sampling. The following scheme shows the general trend of the results with respect to the relative variability of the different races. The races are arranged in descending order of mean brain-weight in the left-hand columns, and of variability (measured by the coefficient of variation) in the right hand columns. The lists are based on the total series.

Mean	*C. of V.*	*Mean*	*C. of V.*
Bohemians	Bavarians	Bohemians	Bavarians
Swedes	Hessians	Hessians	Hessians
Hessians	Bohemians	Swedes	Swedes
Bavarians	Swedes	Bavarians	Bohemians

From these lists it would appear that as a general rule the higher the mean brain-weight is, the lower will be the variability. But it must be kept in mind that none of the differences in the variability columns are significant. Taking the extremes, Bavarians and Swedes for the males, and Bavarians and Bohem-

ians for the females, the differences between the coefficients of variability with their probable errors are respectively .526± .217 and .958 ± .337. In these cases the difference is less than three times its probable error and cannot be considered as certainly significant. The lists show merely the general trend of the results. It is possible that with much larger series of brain-weight statistics and consequently reduced probable errors some such relation as that just stated might be definitely proven.

An analytical study of the frequency distributions leads to the conclusion that variation in the weight of the brain may, for *practical* purposes, be considered to follow the "normal" law of the distribution of errors. Some of the series deviate from strict normality, but for the present we cannot do better than use the normal curve. If the mean and the mode do not exactly coincide the mean will be slightly greater than the mode in brain-weight frequency distributions. The various analytical constants for the different series are in close agreement. This fact is strong evidence for the general trustworthiness of the data.

4. *The Correlation of Brain-weight with other Characters.* Brain-weight statistics usually return data for but few other characters; in the majority of cases only sex, age and stature. In two of the series used in this work, viz., the Hessian and the Swedish, this was the case. For these two groups all possible correlations for both sexes and two age groupings ("young" and "total") were determined. This gave as the pairs of characters (a) brain-weight and stature, (b) brain-weight and age, (c) stature and age. Bischoff's Bavarian material furnished, in addition to the above, data on body-weight, so that it was possible to correlate this character with brain-weight and with stature. In the case of the Bohemian material data were furnished from which the correlation between brain-weight and skull length and skull breadth could be determined, in addition to the characters age and stature. The degree of correlation was measured by the well known coefficient,

$$r = \frac{S\ (xy)}{N\sigma_1\ \sigma_2},$$

where x and y are deviations from the means of the two correlated characters ; σ_1 and σ_2 are the respective standard deviations ; and S denotes summation.

The values of the coefficients for the correlation between brain-weight and other characters, together with their probable errors are shown in Table III.[1]

TABLE III.

Brain-weight Correlations.

Character and Series	Swedes			
	♂		♀	
	No.		No.	
Brain-weight and Stature (total)	416	.1830± .0320	233	.3490± .0388
" " " " (young)	262	.1796± .0403	127	.3390± .0530
Brain-weight and Age (total)	416	—.2493 ± .0310	233	— .2336±.0418
" " " " (young)	262	—.1705± .0405	127	— .1512±.0585
Brain-weight and Skull length (young)	--		--	
" " " " breadth (young)	---		---	
Brain-weight and Body-weight (total)	--		--	

Character and Series	Hessians			
	♂		♀	
	No.		No.	
Brain-weight and Stature (total)	475	.1823± .0299	281	.1828 ±.0389
" " " " (young)	291	.1741 ± .0383	173	.1809 ±.0496
Brain-weight and Age (total)	475	—.1673 ± .0300	281	—.3598 ± .0350
" " " " (young)	291	—.0750± .0393	173	— .1650 ±.0499
Brain-weight and Skull length (young)	---		---	
" " " " breadth (young)	---		---	
Brain-weight and Body-weight (total)	---		---	

Character and Series	Bohemians			
	♂		♀	
	No.		No.	
Brain-weight and Stature (total)	---		---	
" " " " (young)	266	.2034± .0397	133	.2168±.0557
Brain-weight and Age (total)	372	—.2045 ± .0335	197	—.2558 ±.0449
" " " " (young)	--		--	
Brain-weight and Skull length (young)	299	.5482 ± .0273	159	.3604 ±.0465
" " " " breadth (young)	299	.4655 ± .0306	159	.5041 ±.0399
Brain-weight and Body-weight (total)	--		---	

[1] It will be remembered that the limiting values of the coefficient of correlation are o and ± 1, o indicating entire absence of correlation between the two variables, and + 1 and — 1 indicating perfect positive and negative correlation respectively.

Character and Series	Bavarians			
	♂		♀	
	No.		No.	
Brain-weight and Stature (total)	365	.1664 ± .0343	241	.2236 ± .0413
" " " " (young)	---	-------------	---	-------------
Brain-weight and Age (total)	529	—.1225 ± .0290	323	—.2405 ± .0354
" " " " (young)	365	—.0100 ± .0353	238	0114 ± .0437
Brain-weight and Skull length (young)	---	-------------	---	-------------
" " " " breadth (young)	---	-------------	---	-------------
Brain-weight and Body-weight (total)	365	.1671 ± .0343	241	.2260 ± .0412

It will be seen that a generally low degree of correlation exists between brain-weight and the other characters studied. The coefficients run lower even that those of skull characters (cf. Macdonell :04, Table X) and markedly below those between different characters of the long bones (cf. on this point Lee and Pearson :01, p. 229). On the other hand the brain-weight correlations give values of the same general order of magnitude as those found by Greenwood (:04) for various abdominal and thoracic viscera. The values of the correlation coefficients for particular cases will be discussed in the sections of the paper which follow.

5. *Brain-weight and Sex.* All brain-weight statistics agree in showing that the brain of the male is absolutely heavier than that of the female. I have found the sexual difference in mean brain-weight to be practically the same (taking into account the probable errors) for all the races studied, whether considered absolutely or relatively. The absolute differences (in grams) in the mean brain-weight of the sexes are shown in Table IV.

TABLE IV.

Male mean—Female mean

	"Total" series	"Young" series
Swedes	147.8	145.8
Bohemians	143.9	146.2
Bavarians	142.8	133.6
Hessians	131.9	125.6

Only a part of this sexual difference is to be accounted for by differences in other bodily characters. If we take a group of males and a group of females having the same

mean age and stature, we shall get rid of only about 29 per cent. of the usual sex difference in brain-weight. Similarly, if the male and female groups have the same mean stature and body weight only about 28 per cent. of the usual sex difference in brain-weight will be removed. Finally, if the male and female groups have the same mean skull length and skull breadth about 47 per cent. of the sex difference in brain-weight will be removed. It will be understood that the effect of these selections is not cumulative in the proportions given by the percentages. In other words, a selection of males and females to the same type with respect to characters other than brain-weight (excepting, of course, other characters of the brain itself) will reduce the usual sex difference in this character by probably less than 50 per cent. So then we must conclude that the adult female human brain weighs less than that of the adult male, irrespective of differences in other bodily characters.

The sexes are equally variable in brain-weight. This is shown by Table V. which gives the differences between the male and female coefficients of variation with the probable errors of the differences. The value tabulated is the male minus the female constant in each case.

TABLE V.
Relative Variability of the Sexes.
Male—Female.

Race	Coefficients of Variability	
	"Total" series	"Young" series
Bohemian	.427 ± .320	.740 ± .375
Hessian	—.029 ± .293	—.036 ± .366
Bavarian	—.222 ± .254	.546 ± .305
Swede	—.451 ± .310	—.600 ± .422

In three cases out of the eight the male has a larger coefficient of variation than the female, but in no instance can the difference between male and female coefficients be considered significant when compared with the probable error. Therefore we are forced to the conclusion stated in the preceding paragraph.

The weight of the brain is generally more highly correlated with other characters in the female than in the male.

6. *Brain-weight and Age and Stature.* The correlation of brain-weight with age is negative. This is an expression of the fact that the weight of the brain diminishes with advancing years. The point which I especially wished to investigate was the character of the regression of brain-weight on age. If this regression is linear throughout it means that the diminution in brain-weight accompanying increase in age is steady and uniform throughout the adult period of life. This I found to be the case within the limits of error from random sampling. Beginning with about age 20 there is a steady and uniform, through gradual, decline in brain-weight with advancing years, up to age 80 which was the upper limit of the period investigated. For all practical purposes the regressions may be taken to be strictly linear. The paucity of material makes it impossible to determine with great precision the form of the regression line, but it is quite clear that no simple curve will represent the regression of brain-weight on age for the series here studied better than does a straight line. A full discussion of this important matter with diagrams of the actual regression lines together with the analytical data will be found in the complete paper. The increased rate of decline of brain-weight beginning at about age 50, which was expected, was not found.

The correlation between brain-weight and age is in all series except the Swedish higher for the females than for the males. It is suggested that in this higher correlation we may have ''an expression in a particular case of a greater general 'evenness' of the bodily changes accompanying increasing age in the female, which in turn might be due to the generally more even environmental conditions to which women are subjected. It is noteworthy in this connection that the correlation in respect to duration of life is generally higher between pairs of female relatives than between pairs of male relatives'' (BEETON and PEARSON :01, p. 60).

The correlation between brain-weight and stature is posi-

tive throughout, denoting that generally with any deviation from the mean in stature, there is associated a deviation in the same sense from the mean brain-weight. The regressions are sensibly linear. The coefficients of correlation between brain-weight and stature and brain-weight and age are of the same general order of magnitude, or, in other words, weight of brain is only slightly more closely associated with size of body (as measured by stature) than it is with age. The relations of stature and age to brain-weight are very clearly shown in the characteristic equations (vide infra, p. 478).

7. *Brain-weight and Body-weight.* The correlation of brain-weight with body-weight is positive, and of about the same degree as the correlation of the former with stature. The regression approaches somewhat more closely to strict linearity in the case of body weight than in the case of stature. A unit change in body weight is associated with a smaller change in brain-weight than is a unit change in stature.

8. *Brain-weight and Skull Characters.* The correlations between brain-weight and skull length and skull breadth are positive and give the highest values for the coefficients of any of those studied. For certain reasons discussed in the complete paper it seems possible that the values obtained for these correlations from the Bohemian statistics are still somewhat too low. The regressions are sensibly linear. The correlation between brain-weight and skull length and breadth is somewhat less close than that between skull capacity and length and breadth. This is shown in Table VI.

TABLE VI.

Race	Brain-weight and Skull Length		Brain-weight and Skull Breadth	
	♂	♀	♂	♀
Bohemian	.5482 ± .0273	.3604 ± .0465	.4655 ± .0306	.5041 ± .0399
	Skull Capacity and Length		Skull Capacity and Breadth	
English[1]	.597 ± .051	.691 ± .040	.631 ± .048	.646 ± .044
Naqada[2]	.501 ± .054	.599 ± .039	.434 ± .058	.532 ± .044
German[3]	.515 ± .050	.689 ± .037	.672 ± .037	.706 ± .034
Aino[3]	.893 ± .016	.663 ± .053	.561 ± .053	.502 ± .070

[1]MACDONELL, :04.   [2]FAWCETT, :02.   [3]LEE and PEARSON, :01.

More and better material for determining the relation between brain-weight and skull characters is much to be desired.

9. *The Weight of the Cerebrum.* The BOYD-MARSHALL English material placed at my disposal by Professor DONALDSON made it possible to determine the variation in this character, and its correlation with age and stature. The cerebral hemispheres are markedly more variable in weight than is the entire encephalon. This character is slightly less closely correlated with stature and age than is the weight of the entire encephalon.

10. *Characteristic Equations.* Exact comparison of the brain-weight in different races has hitherto been impossible on account of the lack of precise methods of allowing for the influences of age, stature, sex and other bodily differences. A knowledge of the degree of correlation existing between brain-weight and these other characters at once places in our hands the data through which such exact comparisons can be made. With a knowledge of the coefficients of correlation and the standard deviations we can form so-called "characteristic equations" which will give the probable brain-weight for arrays of individuals of given types of the various other characters. Such equations, besides enabling us to predict probable brain-weight from a knowledge of other characters, also make clear the relative influences of these characters on the weight of the brain.

I have put together here all the characteristic equations calculated in the course of the work. In these equations the letters have the following significance :

W = probable brain-weight in grams.
A = known age in years for the period 15 (or 20) to 80.[1]
a =   "   "   "   "   "   "   "   50.[1]
S = stature in centimetres, for individuals between 15 (or 20) and 80 years.[1]
s =   "   "   "   "   "   "   "   "   " and 50 years.[1]
W_B = weight of body in kilograms
L = length of skull in millimetres
B = breadth   "   "   "
Σ = standard deviation (in grams) of the array having W as the mean.

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[1] The equations containing the letters a and s are based on the "young" series, and those containing A and S on the "total" series.

Equations   Σ

(1) Swedish	♂	W = 1487.783 — 1.939 A	102.972
(2)	"	♂	W = 1501.411 — 2.372 *a*	107.582
(3)	"	♀	W = 1326.475 — 1.549 A	97.969
(4)	"	♀	W = 1340.438 — 1.938 *a*	104.329
(5) Hessian	♂	W = 1439.734 — 1.119 A	111.087
(6)	"	♂	W = 1432.497 — .847 *a*	111.014
(7)	"	♀	W = 1361.067 — 2.259 A	95.512
(8)	"	♀	W = 1339.298 — 1.735 *a*	100.445
(9) Swedish	♂	W = 915.054 + 2.859 S	104.533
(10)	"	♂	W = 919.374 + 2.914 *s*	107.405
(11)	"	♀	W = 421.994 + 5.234 S	94.421
(12)	"	♀	W = 451.643 + 5.121 *s*	99.294
(13) Hessian	♂	W = 913.592 + 2.857 S	110.787
(14)	"	♂	W = 950.214 + 2.723 *s*	109.628
(15)	"	♀	W = 834.624 + 2.714 S	100.643
(16)	"	♀	W = 894.031 + 2.460 *s*	100.161
(17) Bavarian	♂	W = 836.667 + 3.127 S	118.452
(18)	"	♀	W = 627.157 + 3.824 S	103.562
(19) Swedish	♂	W = 1091.021 + 2.288 S — 1.755 A	101.819
(20)	"	♂	W = 1030.715 + 2.352 *s* — 1.856 *a*	106.477
(21)	"	♀	W = 561.433 + 4.679 S — 1.078 A	93.066
(22)	"	♀	W = 533.407 + 4.854 *s* — 1.092 *a*	98.923
(23) Hessian	♂	W = 942 154 + 2.989 S — 1.181 A	108 992
(24)	"	♂	W = 926.586 + 3.107 *s* — 1.318 *a*	108.889
(25)	"	♀	W = 1005.607 + 2.244 S — 2.173 A	94.261
(26)	"	♀	W = 974.382 + 2.345 *s* — 1.829 *a*	98.883
(27) Bavarian	♂	W = 1263.308 + 1.886 W$_B$	118.439
(28)	"	♀	W = 1121.621 + 2.265 W$_B$	103.495
(29)	"	♂	W = 917.748 + 2.234 S + 1.355 W$_B$	117.711
(30)	"	♀	W = 741.078 + 2.646 S + 1.593 W$_B$	102.432
(31) Bohemian	♂	W = 8.589L — 52.650	96.548
(32)	"	♂	W = 8.076B + 253.596	102.170
(33)	"	♀	W = 6.215L + 264.265	88.466
(34)	"	♀	W = 8.646B + 68.434	81.908
(35)	"	♂	W = 6.751L + 5.082 B — 489.649	99.745
(36)	"	♀	W = 4.696L + 7.766 B — 602.994	77.893

A study of these equations shows at once the precise rela-
tion of each of the other characters, both singly and combined,
to brain-weight. The equations afford a means of scientifically
comparing the mean brain-weight of different races, since by
their use we can, in effect, reduce the races to be compared to
the same base with reference to other characters. This use of
the equations is illustrated for a specific instance in Table I,

supra. Numerous other uses to which they may be put are illustrated in the complete paper.

In using these equations the following points should be kept in mind:

(a) The equations give the *probable mean brain-weight* of an array of given type in respect to other characters They are therefore not to be depended on to predict *individual* brain-weights.

(b) They are strictly *intra-racial* equations.

(c) The male and female equations are not interchangeable.

(d) On material comprising individuals between the ages of 15 and 50 the equations based on the "young" series should be used.

11. *Concluding Remarks.* In concluding I desire to call attention to the following points.

(a) The essential agreement between the four different races studied in respect to the biometric constants for variation and correlation in brain-weight is noteworthy. This agreement in the statistical constants from four series of data so divergent in their origin as those treated in this work cannot reasonably be held to be fortuitous. It can only mean that there are definite laws underlying variation in the weight of the brain which are not fundamentally different from the laws of variation for the other characters of the body.

(b) There is no evidence that intellectual ability and the weight of the brain are in any degree correlated in normal individuals.

(c) There is need for more and larger collections of brain-weighings, in which close attention is paid to the homogeneity of the material, and to the recording of other subsidiary data in addition to brain-weight. In comparison with the series of brain-weighings available at present, a collection which should record the following facts would be almost ideal.

1. Brain-weight, by the standard method.
2. Race. In this the more essential detail given the better.
3. Country of residence during adult life.

4.   Occupation (as an index of social status).
5.   Immediate cause of death.
6.   Chronic illnesses of adult life.
7.   Stature
8.   Body-weight.
9.   Head length.   } All measurements made
10.   "   breadth. | before skull is opened,
11.   "   height. | and with hair removed
12.   Maximum horizontal circumference of head   } at points of contact.
13.   Age.
14.   Sex.

This list is presented with the hope that any future worker who may be about to undertake the labor involved in obtaining a large mass of human brain-weight statistics will at least consider the points raised.

It gives me pleasure to acknowledge my indebtedness to the Carnegie Institution for aid in carrying on this and other biometric investigations.

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THE RELATION BETWEEN THE OCCURRENCE OF WHITE RAMI FIBERS AND THE SPINAL ACCESSORY NERVE.

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(With an Addendum by J. PLAYFAIR MCMURRICH)

With One Figure.

In two important papers published in 1886 and 1889 GASKELL pointed out that the spinal accessory nerve in the dog contained in its upper part fine calibered fibers resembling those which formed the visceral efferent fibers of the thoracic nerves, and concluded that these fibers represented the white rami communicantes of the upper cervical nerves. Furthermore he revived, in a new form, the view propounded long before by BELL, in supposing that instead of but two roots, each segmental nerve of the body possessed in addition visceral roots, which, so far as their efferent fibers were concerned, were associated with a lateral column of cells in the central nervous system. Throughout a considerable portion of the spinal region these visceral efferent fibers form the white rami communicantes ; in the cranial region they are represented by those fibers which, since the embryological studies of HIS demonstrated so clearly their distinctness, are generally known as the lateral motor roots. And since the fibers of the lower roots of the spinal accessory belong to the lateral motor series, and according to GASKELL's view the upper roots represent white rami communicantes, there follows the conclusion that a correlation should obtain between the spinal accessory nerve and the occurrence of white rami passing from the spinal nerves to the sympathetic cord.

In the dog GASKELL found in the anterior roots of the spinal nerves from the 10th to the 25th, large numbers of

very fine calibered medullated fibers, their diameter varying from 1.8μ to 2.7μ with a few reaching $3.6\,\mu$. He found also that the tenth nerve, i. e., the second thoracic, in which these fibers first appeared, was the uppermost one which had a white ramus communicans connected with it and furthermore he found that this white ramus was composed almost entirely, so far as its medullated fibers were concerned, of fibers of a similar calibre to those first occurring in the anterior root of the tenth nerve. The conclusion naturally followed that the fine calibered fibers of the anterior roots were the white rami fibers and that the first group of such fibers given off from an anterior spinal root was that of the second thoracic.

If these conclusions be correct, then it is clear that in the dog there is a distinct gap between the first nerve which possesses a white ramus and the level at which the lowest root of the spinal accessory nerve arises, this root being given off at about the level of the seventh cervical nerve, three segments above the level of the first white ramus. Such a condition does not accord with Gaskell's view as to the significance of the spinal accessory and it seemed that it might be of interest to investigate the relations of the two structures, spinal accessory and white rami, in other mammals with a view to ascertaining whether the discord was of general occurrence or whether some correlation really existed.

For this purpose it seemed advisable to select first of all some form in which the origin of the lowest root of the spinal portion of the spinal accessory occurred at a decidedly different level than in the dog. Bischoff (1832) in his comparative study of the spinal accessory found that in mammals there was a considerable difference in the distance to which the nerve descended into the cervical region. Thus, he found that it descended in the weasel to about the level of the second cervical nerve ; in the mole, rat and marmot to that of the third cervical ; in the rabbit to that of the fifth cervical ; in the stone-marten, stag, cat, wolf and man to that of the sixth cervical ; and in the pig, dog, and calf to that of the seventh cervical. Having regard to these data the rat was chosen as a suitable

form for study, especially as it was one readily obtained ; and a study of the distribution of small medullated fibers in the anterior roots of the cervical spinal nerves and in the rami communicantes with reference to the lowest root of the spinal accessory was made in that form.   Some observations were also made upon the cat and dog, but rats fully grown, formed the principal object of study.

Before proceeding to consider the conditions in the rat it is necessary to define what is meant by a white ramus fiber. GASKELL limited the term to small fibers which were distinctly grouped in bundles, and on this basis made a special point of the occurrence of the uppermost white ramus communicans in connection with the second thoracic nerve.   But is such a limitation justifiable ?   Must it be supposed that fibers of the same quality are always grouped together in distinct bundles ?   Such does not seem to be the case throughout the central system and from what is known as to the association in bundles of fibers of very different origin in both the central and peripheral systems —e. g. the so-called mesial fillet fibers with the fillet in the central system, and the chorda tympani with the lingualis fibers in the peripheral system—it would seem that the mode of grouping of fibers so far as their quality or origin is concerned, is, to some extent at least, fortuitous.   It seems quite possible that when but a relatively small number of white rami fibers exist, they may not form a distinct bundle, but may be incorporated in a single trunk with grey rami fibers and may, if their number be very small, be scattered among such fibers.   In other words, it is possible that the ordinary use of the terms white and grey ramus is merely relative, indicating merely the preponderance in the nerve trunk of one or the other variety of fibers.

The observations of HARMAN (1900) on the occurrence of white rami fibers in man makes this possibility very prominent and my observations upon the rami communicantes of the lower cervical and upper thoracic nerves of a dog are also of interest in this connection.

In sections of the ramus connected with the 6th cervical nerve four distinct bundles were found.   Three of these were

quite small, while the fourth was large, its area exceeding considerably that of the other three combined. The three small
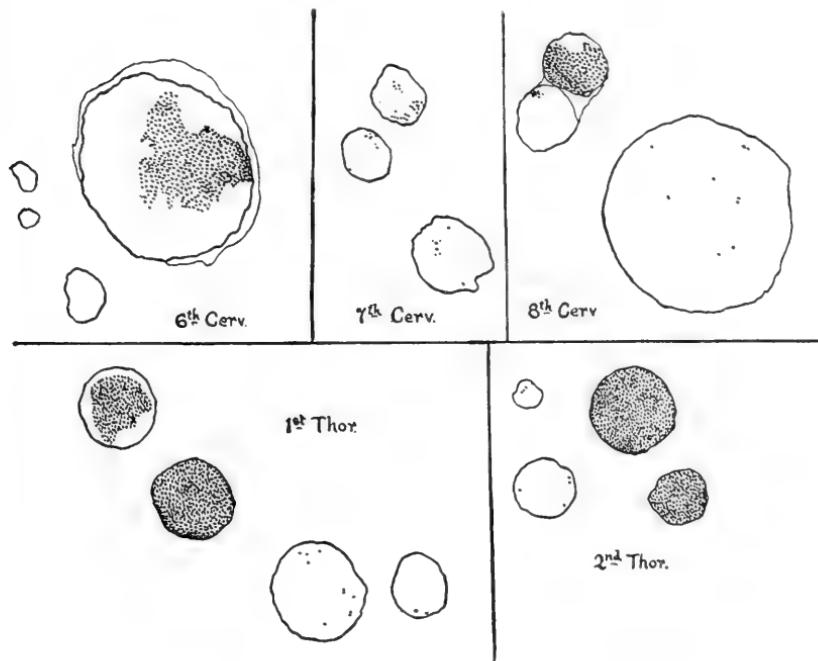
DESCRIPTION OF FIGURE. Transverse sections of the rami communicantes of the sixth cervical to the second thoracic nerves in the dog. The outlines were traced with a camera lucida; the shaded areas represent white fibers and the unshaded grey, but no attempt has been made to represent the actual number of white fibers in the rami in which they are abundant, the eighth cervical nerve, for example, containing more white rami than the sixth in which they are interspersed with grey fibers.

bundles were wholly composed of non-medullated fibers, but the large one, though mainly non-medullated, contained imbedded in its central portion a large number, at least 250, small calibered medullated fibers. On superficial inspection, such a ramus would undoubtedly appear to be a gray ramus since the white fibers were almost entirely invested by the non-medullated ones.

The ramus of the seventh cervical nerve consisted of three bundles, two of which were entirely grey, while the third contained a few, about 25, medullated fibers. The eighth ramus

consisted again of three bundles, one of which was large and grey, containing only about half a dozen small medullated fibers, the second small and almost entirely grey, while the third was almost entirely composed of white fibers, although two small groups of grey fibers occurred at its periphery. These two small bundles were fused in the upper part of the ramus. The first thoracic ramus consisted of five bundles, one of which was exceedingly small, consisting of not more than about one dozen fibers, six of which were medullated. Of the other bundles two were almost entirely grey, containing each from ten to twelve medullated fibers, while the other two were mainly white, one entirely so, the other however containing a considerable number of grey fibers. Finally in the second thoracic ramus four bundles were present, two of which were almost entirely grey, containing each only a half dozen small white fibers, while the other two were entirely white.

In connection with the second thoracic there are two bundles which may properly be designated white rami, in connection with the first thoracic one, and in connection with the three lower cervical none. But in each of the cervical rami and in an additional bundle of the first thoracic small white fibers exist which are in no wise different either in appearance or size from fibers composing recognized white rami. Only by determining the origin and termination of these fibers can it be definitely decided that they are really white rami fibers, but if there is anything to be concluded from their size and their similarity to the fibers of the white rami, then they are undoubtedly of the same nature as these latter, and they will be termed white rami fibers in what follows.

Evidence as to the nature of the fibers may be derived from physiological experimentation. The observations of NAW-ROCKI and PRZYBYLSKI (1891) and more especially of LANGLEY (1892) certainly do not favor the view that the fibers in question are white rami fibers, since they found that in the cat, in which the conditions are very similar to those obtaining in the dog, no dilatation of the pupil resulted from stimulation of the anterior roots of nerves above the eighth cervical, LANGLEY

(1892) indeed, obtaining no response to stimulation of roots above the first thoracic. And furthermore the latter author found no evidence of the existence of vaso-constrictor fibers for the head, of secretory fibers for the submaxillary gland or of accelerator fibers for the heart in the anterior roots of nerves above the first thoracic.

It is to be noted, however, that these results were obtained by stimulation of the anterior roots of the spinal nerves. At an earlier date FRANCOIS-FRANCK (1878), working in MAREY'S laboratory obtained quite different results by the direct stimulation of the rami communicantes. He isolated in the cat the lower cervical and upper thoracic rami, and after severing their connections with the roots of the spinal nerves stimulated each one independently, with the result that he obtained dilatation of the pupil on stimulation of the rami of all the nerves from the sixth thoracic to the fifth cervical inclusive, and he concluded that "la moelle cervico-dorsale, entre le niveau de la 5^{me} cervicale et de la 6^{me} dorsale, fournit au ganglion 1re thoracique des rameaux convergentes qui contiennent tous, en plus ou moins abondance, de filets irido-dilatateurs."

These results are clearly much more in harmony with the anatomical observations recorded above, and it becomes an interesting question to determine the cause of the discrepancy between the results which followed stimulation of the anterior roots and those following stimulation of the white rami. This question did not, however, fall within the scope of the present study as it was originally planned, and I shall now proceed to consider the relations which exist between the roots of the spinal accessory nerve and the occurrence of white rami fibers in the rat.

Observations on Rats.

In five rats the spinal cord was exposed by carefully cutting away the neural arches of the vertebrae, and the spinal accessory was then traced down the cord with the aid of a dissecting microscope. In each animal the lowest roots on both sides emerged from the cord just above the roots of the fourth

cervical nerve, that is to say, somewhere about the level of the third nerve as described by BISCHOFF.

From two individuals the anterior roots of the second, third, fourth and fifth cervical nerves were removed, stained in osmic acid, imbedded, after the usual preliminary treatment, in paraffin and cut into 10 μ sections. All of the roots were composed principally of large medullated fibers, having a diameter varying from 10 to 20 μ, but in addition there could be observed in each a small number of fibers whose diameter was less than 4 μ, many of them not exceeding 2 μ. Even on superficial examination, however, it could be perceived that these small fibers were much more numerous in the lower than in the upper roots and counts which were made of the fibers with a diameter of 4 μ or less gave the following results.

Roots	Rat No. I	Rat No. II
2d cervical	130	168
3d "	105	126
4th "	380	363
5th "	432	449

It is evident then, that a sudden increase in the number of small medullated fibers occurs in the anterior root of the fourth cervical nerve, that is to say, in the nerve immediately below the emergence of the last root of the spinal accessory.

The rami communicantes were next dissected out in three other rats and placed in osmic acid. The rami which were connected with the three uppermost cervical nerves failed to show any blackening with the osmic and may consequently be regarded as composed solely of gray rami fibers. With the succeeding rami, however, the case was different, a distinct blackening taking place, and on sectioning these rami it was found that they were largely composed of medullated fibers, a considerable number being of large size, measuring from 10 to 16 μ in diameter, scattered among which were numerous fibers, arranged to some extent in groups and of the same general diameter as the small fibers of the anterior roots. Counting these, it was found that they numbered in one individual 195 in the fourth ramus and 220 in the fifth.

Comparing these figures with those obtained from a count of the anterior root fibers it will be seen that they account to a very considerable extent for the increase of small fibers in the fourth anterior root, a conclusion which may be clearly seen from the following table.

Nerve	Medullated fibers less than 4μ in diameter	Medullated fibers less than 4μ in ramus communicans
2d cervical	130—168	None
3d "	105—126	None
4th "	380—363	195
5th "	432—449	220

It must be remembered however, that the counts of the anterior root fibers and those of the white rami fibers were made upon different individuals and the results show only approximately the correlation which obtains. It seems that in the anterior roots of all the upper cervical nerves there is a considable number of small fibers whose diameter is less than 4μ, but that a sudden increase in the number occurs in the anterior root of the fourth nerve and that this increase is fairly proportional to the number of fibers of a similar size in the corresponding ramus communicans. Furthermore, this increase occurs in the first nerve below the lowest root of the spinal accessory.

Observations on Cats.

The spinal accessory of the cat, according to BISCHOFF's observations, descends to the level of the sixth cervical nerve. Concerning the occurrence of white rami fibers in this animal the anatomical data are rather scanty, notwithstanding its extensive employment in physiological experimentation.

LANGLEY, it is true, paid some attention to this side of the problem, but apparently confined his attention mainly to those rami communicantes which without microscopical examination could be recognized as composed largely of medullated fibers. He says "in the Cat and Dog, the uppermost *obvious* white ramus is that for the IInd thoracic; but with a little trouble one, two, or three fine white strands can be seen stretching from the Ist thoracic nerve to the ganglion stellatum. When these are

hardened in osmic acid and sections cut, they are seen to have the characters of white rami ; that is, they consist chiefly of small medullated fibers collected in bundles, with a few medium or medium sized fibers ; between the bundles are a variable number of non-medullated fibers ; besides these there one or more grey rami, *i.e.*, bundles consisting chiefly of non-medullated fibers, but containing scattered medullated fibers."

These results are entirely in harmony with the author's experimental observations and show a marked discrepancy between the occurrence of efferent white rami fibers and the development of the spinal accessory.

In four out of five cats examined in connection with the present study, the level of the lowest root of the spinal accessory agreed with that assigned to it by BISCHOFF, that is to say, it occurred at the level of the sixth cervical nerve. In the fifth individual, however, the nerve of the left side extended down the cord only to the level of the fifth cervical nerve, that on the right side agreeing with the findings in the other individuals.

In two of the four individuals in which the development of the spinal accessory was symmetrical in the two sides, it was found that the ramus communicans given off from the sixth cervical nerve contained a very few scattered medullated fibers. That from the seventh nerve however, contained a large number of white rami fibers. In the fifth animal, in which the development of the spinal accessory was unsymmetrical, sections were made of the anterior roots of the spinal nerves after treatment with osmic acid, but unfortunately the rami were not studied, and as regards the anterior roots, it was not found possible to make a count of the smallest fibers, which could be regarded as sufficiently accurate for record. It was certain, however that a marked increase in the number of these fibers occurred in a definite anterior root on each side and this increase was correlated with the level of the lowest root of the spinal accessory. Thus it was found that on the left side, on which the spinal accessory descended to the level of the fifth nerve, the sudden increase of small fibers occurred in the anterior root of the sixth nerve, while on the right side, in which the access-

ory descended to the level of the sixth nerve, the increase did not occur until the seventh nerve. These relations may be expressed in tabular form thus:

	Level of lowest root of spinal accessory.	Anterior root in which increase of small fibers occurs.
Left side	5th nerve	6th nerve
Right side	6th nerve	7th nerve

These observations in the cat are by no means so conclusive as those made upon the rat, but nevertheless they harmonize admirably with them, and the case of the fifth cat is especially interesting as showing that the correlation of the white rami fibers with the origin of the lowest root of the spinal accessory nerve occurs even in cases of individual variation.

Addendum.

From the above observations there appears to be, in both the rat and the cat, a sudden increase in the number of white rami fibers in the ramus communicans of the nerve which immediately succeeds the last root of the spinal accessory nerve, and the conditions demanded by Gaskell's supposition are fulfilled. It does not, however, necessarily follow that the significance which Gaskell assigns to the spinal accessory is the correct one. It may be true that the cranial lateral motor roots are serially homologous with the visceral motor roots, i. e., the white rami fibers of the cord; indeed, there is much to recommend such a view. But that the spinal accessory, or to be more precise, the cervical portion of that nerve, actually represents the white rami fibers of the upper cervical spinal nerves is more than doubtful.

It is becoming more and more apparent that the classification of the spinal accessory as a distinct unit in the series of cranial nerves is erroneous; it is rather merely a portion of the vagus, whose continuation down the spinal cord is no more remarkable than the downward extension of the spinal tract of the trigeminus. It is true that the fibers of the latter nerve pursue their downward course in the substance of the central

nervous system, while the spinal accessory fibers emerge from the cord, but it must be remembered that in the one case the fibers in question are afferent and in the other efferent in quality. In all its morphological and physiological characters, especially when studied from the comparative standpoint, the accessory is closely related to the vagus, and the view, so strongly supported by FÜRBRINGER, that the accessory is really a portion of the vagus, its nucleus being merely a downward extension of the vagus nucleus, seems to represent the true significance of the nerve.

Whether or not the downward extension of the vagus nucleus be dependent upon the development of the trapezius and sterno-mastoid muscles, as the evidence presented by FÜRBRINGER seems to indicate, it is certain that comparative anatomy shows us a gradually increasing size of the vagus nucleus and its gradual extension into the spinal region. What the cause which determines the direction of the extension may be is at present unknown, but it is to be noted that the motor vagus nucleus is a lateral nucleus and its direct prolongation downward would therefore bring it into most intimate relation with the cell column from which the spinal white rami fibers take their origin. In its continued downward progress it may be supposed that it would gradually displace the majority of the cells of the sympathetic column throughout the spinal segments it traversed, forcing them to a lower level, so that throughout the region occupied by the extended nucleus, white rami fibers would be either wanting or few in number, while below the termination of the nucleus there would be a sudden increase in their number. This is exactly the condition which the results recorded above seem to show.

There is one point, however, which such an explanation fails to clear up, namely, the existence of a second somewhat sudden increase in the number of white rami fibers in connection with the first and second thoracic nerves. The fact that this second outflow begins at about the level of the lowest nerve participating in the formation of the brachial

plexus, and that it ceases at about the level of the beginning of the lumbo-sacral plexus, has suggested its dependence in some way upon the plexuses, a view which has been especially emphasized by HARMAN with reference to the upper limits of the outflow. The exact significance of the interdependence remains, however, obscure; but granting its existence, it still leaves room for the significance which has been assigned above to the upper outflow, and it would seem that there are two factors influencing the occurrence of white rami fibers in the cervical region, one of which is the development of the spinal accessory nerve, while the other is associated with the development of the brachial plexus.   J. PLAYFAIR MCMURRICH.

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RESPIRATION AND EMOTION IN PIGEONS.

By John E. Rouse.

(*From the Harvard Psychological Laboratory.*)

CONTENTS.

I. Problem and Method.

Both daily observation and numerous expressions in literature indicate the highly developed emotional life of birds. All other lower animals, even dogs, are inferior to them in this regard. Desiring to investigate this interesting subject, I undertook an experimental study of the respiratory reactions of the pigeon, an animal which is easily handled and which readily adapts itself to laboratory confinement.

As a process through which to study mental phenomena, breathing[1] combines two important advantages:—first, it is *variable*, being highly sensitive not only to changes of the blood, but also to impulses from the peripheral or from the central nervous system; and, secondly, its alterations may be *easily recorded* pneumographically. The value of the pneumograph-

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[1] The physiology of respiration is well summarized by Starling in Schaefer's Text-Book of Physiology, II, 274-312.

ic method, especially in the study of feeling[1] and attention,[2] has long been recognized in human psychology, although the numerous difficulties involved in the interpretation of animal reactions have discouraged its use by comparative psychologists.

In the experiments here to be reported an effort was made to obviate some of these difficulties by studying, for purposes of comparison, wholly different forms of reaction *to the same stimuli.* It is true that respiratory responses *taken by themselves* are of little value in the investigation of animal mind. But they assume a different aspect when correlated with directly comparable responses of a wholly different order. Thus, for example the influence of certain odors upon animal breathing would become material for psychology if we knew the free behavior of the animals in the presence of these same stimuli. Although the results of the present study are few and subject to correction[3] it is hoped that they may lead to the use of this method in similar investigations.

I wished to study the pigeon's respiratory movements by means of a pneumographic tracing secured under conditions as natural as possible. Hence a light, delicate apparatus was constructed *to be worn* by the animal when standing at its ease in the cote. The extreme difficulty of fastening the apparatus, however, made it necessary to test the bird in a kind of narrow nest, formed by cutting an oval opening in a fixed horizontal board (see Fig. 1, *M.*). The breast could thus be exposed below and its vertical, or sterno-vertebral, breathing movements secured by a tambour and recorded by the usual method.[4] No attempt was made to register other kinds of breathing

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[1]See the interesting study by Zoneff and Meumann, Ueber die Begleiterscheinungen psychischer Vorgänge in Athem und Puls, *Philosophische Studien,* **18,** 1-113, 1901.

[2]See Lehmann's paper, Ueber die Beziehung zwischen Athmung und Aufmerksamkeit, *Philosophische Studien,* **9,** 66-95, 1894.

[3]I refer especially to the relative percentages given in Table III. A larger number of animals, tested under conditions more favorable, would give more reliable averages.

[4]Langendorff, O. Physiologische Graphik. *Leipzig und Wien,* 1891.
Binet and Henri. La fatigue intellectuelle. *Paris,* 1897.

movements.[1] The animal's feet were so troublesome that it was found to be best to secure them in an easy position by means of tape fastened to hooks behind. Great care was taken in placing the animal in the nest, and in adjusting the breast plate from day to day. If the tape were drawn too tightly, the breathing became abnormal; whereas, if drawn too loosely, the vertical position of the bird varied during the experiment and
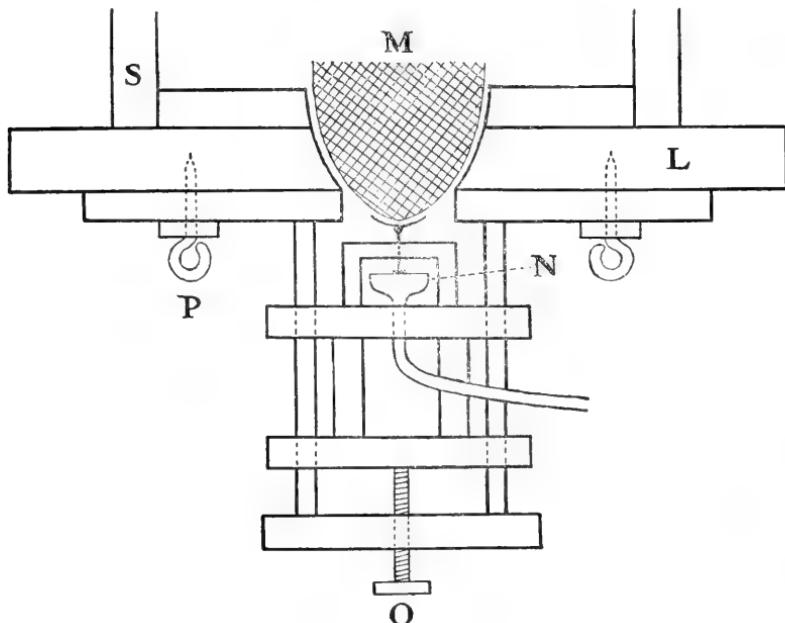
Fig. 1. Pneumograph. *L,* fixed board; *M.,* position of animal; *N,* tambour, adjustment of breast-plate by means of screws, *O* and *P*; *S,* lower edge of box covering bird.

altered the tension of the breast-plate, thus producing modifications in the tracing which were not due to the stimuli. No records were used which appeared untrustworthy. To avoid fright, the room was usually darkened before the bird was handled.[2] In no case was it kept in position longer than was absolutely necessary.

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[1]BERT P. Leçons sur la physiologie comparée de la respiration, 323-4. *Paris,* 1870.

[2]KLEIN, L. W. Methods in Animal Psychology,*American Journal of Psychology*, **10**, 256-279, 1897.

MILLS, W. Nature of Animal Intelligence and Methods of Investigating it, *Psychological Review*, **6**, 262-274, 1897.

Acoustical, olfactory, mechanical and visual reactions were studied. Pistol shots of two intensities and the ringing of an electric bell, were used as acoustical stimuli. Turpentine, ammonia, asafoetida, oil of bergamot and lily of the valley were employed as odors, and were given in small paper pans, placed on a smoothly moving wooden drawer which fitted into the front of the box that covered the bird. Jars were utilized as mechanical stimuli. As visual stimuli red, yellow, green and blue lights were used. These were obtained by use of incandescent lamps, and colored glasses, placed vertically on either side of the animal. Equality of intensity for the different colors was maintained by altering the distance of the source of illumination from color to color. Different intensities were secured by changing lamps.

The time of giving the various stimuli was usually indicated automatically by an electrical signal marker, writing just below the respiration tracing. This was made possible in the case of visual tests, for example, by the use of a double contact key. Rate of drum movement was shown in a third line below, written by a marker which was connected with a metronome. The instrument beat half seconds, and was enclosed in a heavy, felt-lined box.

II. Normal Respiration.

The general contour of the pigeon's normal breathing curve (see Fig. 2) is quite similar to that of man, although the rhythm is much more rapid.[1] The inspiration, or active part of the respiratory act, is usually shorter and more regular in outline than the expiration, or passive part. It begins rapidly, but commences to slacken a little before the middle of its course, and shows a slight pause at the end. The expiration also soon begins to decrease in rate, but the diminution is generally more gradual, and the pause at the end is longer.

In order to determine the relative duration of inspiration

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[1]Starling, op. cit.

and expiration, I measured the ten most regular consecutive respirations which appeared in the daily record of the normal breathing movements of one bird.   Following are the ratios for thirty-two days, stated as expiration to inspiration:—1.50:1, 1.28:1, 1.13:1, 1.04:1, 1.50:1, 1.25:1, 1.55:1, 1.33:1, 1.30:1, 1.22:1, 1.08:1, 1.55:1, 1.46:1, 1.20:1, 1.11:1, 1.82:1, 1.31:1, 1.18:1, 1.23:1, 1.05:1, 1.38:1, 1.11:1, 1.30:1, 1.21:1, 1.13:1, 1.13:1, 1.22:1, 1.33:1, 1.38:1, 1.18:1, 1.05:1, 1.21:1.   General average = 1.27:1.   This is very nearly the ratio found to obtain in human breathing, or 1.20:1.   It will be seen that each day the expiration was longer than the inspiration, though the preponderance varied from day to day.

Some of the days on which records were taken were not consecutive, and it was found that an intermission usually resulted in a considerably increased lengthening of expir-
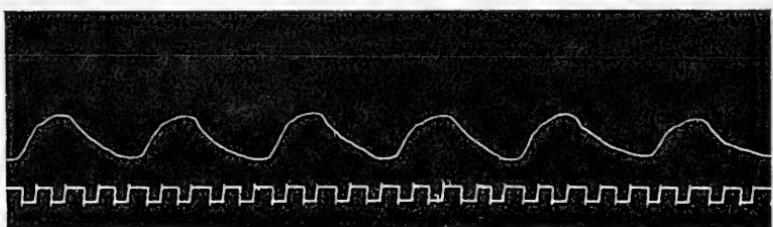
Fig. 2. Normal breathing curve. A single respiratory act extends from hollow to hollow.   The left hand, or shorter, part is the inspiration.   The line is here made too heavy to show minute variations.

ation, although this advance generally disappeared in the next few consecutive days.   The ratio for March 22, for example, was 1.08:1, but for the next four tests (March 25, 26, 28 and 29) it was, respectively, 1.55:1, 1.46:1, 1.20:1, 1.11:1. After a still longer intermission the ratio showed a still greater change, rising to 1.82:1, but rapidly losing again during the next few consecutive days as follows: 1.31:1, 1.18:1, 1.23:1, 1.05:1.   The decrease of ratio was probably due to the fact that there was a tendency for the animal to become gradually accustomed to the general situation on the consecutive days,

and, being less sensitive, to execute the inspiratory, or active, part of the respiration a little less quickly, thus relatively shortening the expiration.

The absolute breathing rate varied considerably from day to day, and sometimes even during an experiment. In case of the above animal the average was 33.6 per minute, though some other pigeons showed a considerably lower rate.

III. General Respiratory Reactions.

1. Acoustical. It was soon noticed that the breathing was sensitive to sounds in the room, especially to those which came from the cages (cooing, flapping, and the like). The reaction given to the sound of the bell was principally a quickening and shallowing,[1] these alterations increasing for a time after the
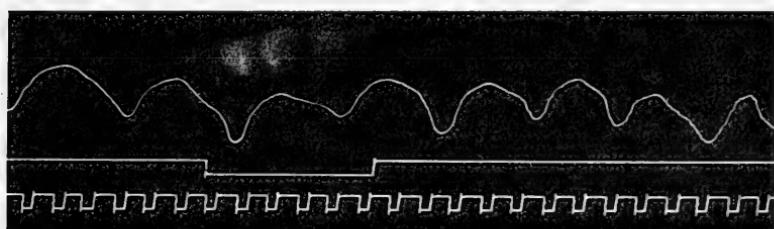
Fig. 3. Reaction to sound of bell. The break in the second line indicates the duration of the stimulus.

end of the stimulation (see Fig. 3.). A pistol shot would result merely in a short pause or temporary hesitation in breathing, followed by a slight quickening of rate. The animal readily became accustomed to these artificial stimuli, and reacted less and less vigorously to them. Yet the sounds which proceeded from the cages in the same room never lost their stimulating effect, perhaps because of their significance. A few instances were noticed in which the reactions seemed to be conditioned by the simultaneous occurrence of a sound stimulus to which the animal was thoroughly accustomed and therefore insensi-

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[1]LEHMANN, A. Körperlichen Aeusserungen psychischer Zustände. *Leipzig,* 1899.

JAMES, W. Principles of Psychology, II, 372-382. New York, 1890.

tive, and certain other stimuli, of low intensity and of themselves incapable of influencing the breathing.[1]

2. *Olfactory.* Oil of bergamot and lily of the valley produced no appreciable reactions. A slight sensitiveness was shown to asafoetida (see Fig. 4). The response was very similar to that caused by the sound of the bell, though much less pronounced. Turpentine and ammonia produced marked reaction, which consisted in quickening and *deepening*, with great irregularity. In some cases the expiration was clearly active and greatly emphasized. Considering how poorly the sense of smell is developed in birds,[2] it may be doubted that these reactions were of a purely olfactory character, although the mucous membranes may have been irritated by the chemicals used.
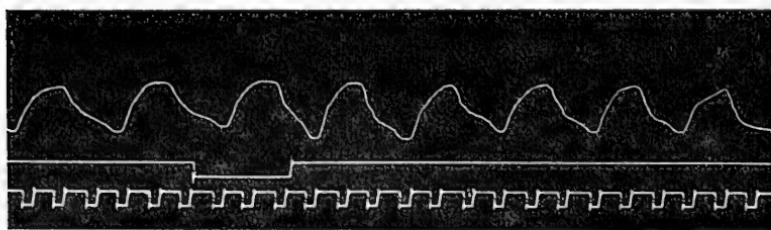
Fig. 4. Reaction to odor of asafoetida.

3. *Mechanical.* The breathing was extremely sensitive to jars of all kinds, whether from the table on which the support rested, or from other parts of the room. Disturbances were caused even by slight vibrations proceeding from remote parts of the building. A slight jar would produce a temporary quickening and shallowing. A violent jar (see Fig. 5) or a jar accompanied by another stimulus, would at first quicken the movement, but later almost completely suspend it, a condition from which the animal would sometimes quickly recover, though often the interruption was more serious. It is a significant fact

[1]DELABARRE, E. B. L'influence de l'attention sur les mouvements respiratoires, *Revue Philosophique*, **33**, 639-649. 1892,

[2]HILL, A. Can Birds Smell? *Nature*, **71**, 318-319. 1905.

XAVIER, R. Le sens de l'odorat chez les oiseaux, *Revue scientifique*, **12**, 144-148. 1897.

'that stimulating the beaks of some diving animals with water, results in a considerable arrest of breathing.
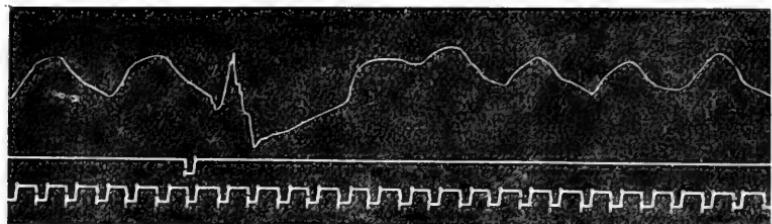
Fig. 5. Reaction to mechanical stimulation.

4. *Visual.* Flashes of light produced considerable disturbance in the breathing curve (see Figs. 6 and 7). The reaction was principally an immediate quickening and shallow-
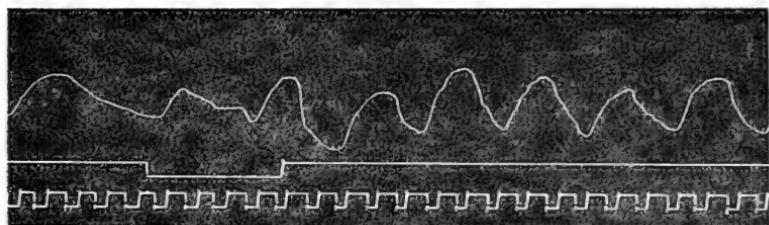
Fig 6. Reaction to red light stimulation.
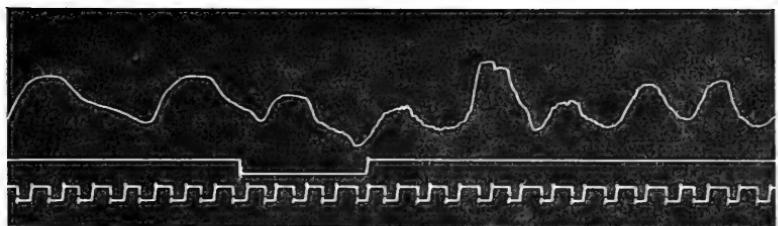
Fig. 7. Reaction to blue light stimulation.

ing, with occasional pauses and minute irregularities. An occasional respiration showed a deepening, but this was probably due to labratory conditions which could not be controlled, for example, jars. No such marked amplitude changes were ob-

served as those which FÉRÉ[1] noticed in human breathing.

The easy control of conditions made vision an excellent field in which to experiment. Hence it was decided to investigate light reactions in some detail. As it is highly important, for purposes of comparison, to study different orders of reaction to given stimuli, I also made a short investigation of the animal's color-preference. This study will be reported in the next section, and the study of respiratory reactions to light in the section next following.

IV. COLOR-PREFERENCE TESTS.

As an index to the pigeon's color-preference, records were kept of the position assumed by the animal when placed in a wire covered, wooden box, half of which was illuminated, from the side, by light of one color, and half by light of a different color but of the same intensity. Use was made of incandescent lamps and colored glasses as in the case of the respiratory reactions, except that the continuous illumination made necessary a water screen to cut off the heat rays. After nine records, half an hour apart, were taken, the glasses were interchanged and the bird's position relatively to the two colors was observed as before. This was repeated with other colors until each of the four colors had been used with each of the other three.

Although the animal's general behavior with regard to the light, especially when going into the box after the colors had been changed, was sometimes very significant, the principal ba-

TABLE I.
COLOR PREFERENCE.

| Animals | Color Choices, with Colors Displayed in Pairs. | | | | | | Total Number of Choices. | | | |
	R, Y	R, G	R, B	Y, G	Y, B	B, G	R	Y	G	B
A	7,11	6,12	5,13	7,11	7,11	8,10	18	25	33	32
B	3,15	5,13	6,12	8,10	9,9	10,8	14	32	31	31
C	3,15	6,12	1,17	4,14	5,13	4,14	10	24	40	34
E	6,12	5,13	5,13	2,16	5,13	14, 4	16	19	33	40
J	6,12	3,15	5,13	12, 6	5,13	9, 9	14	29	30	35
	25,65	25,65	22,68	33,57	31,59	45,45	72	129	167	172

[1] FÉRÉ CH., Note sur les conditions physiologiques des émotions, *Revue Philosophique*, **24**, 566-8. 1887.

sis for deciding as to color-preference was the systematic record. This is given in Table I. Some of the reactions are contradictory, but the general result certainly shows a considerable preference for the colors at the blue end of the spectum.[1]

V. Detailed Study of Respiratory Reactions to Light.

Two distinct classes of respiratory reactions were studied: first, a series of reactions to light of different qualities but of presumably the same intensity ; and, secondly, a series of reactions to light of different intensities but of the same quality. The first set of trials was given with a view to determining the relative stimulating value of light of different qualities ; the second set, to investigate the relation between the reaction and the quantity of the light employed, the stimuli being so applied that the influence of repetition could be observed. Each stimulus was always given as nearly as possible between two respirations, or at the beginning of the inspiration, and was continued two seconds.

Various modifications of the breathing curve were noted, but special attention was paid to alterations in quickness.[2] The rate per minute was estimated for each of the five respirations preceding the beginning of the stimulus, and for each of the ten following it, and the average rate of the two respirations immediately prior to the stimulus was used as a ''normal rate,'' or basis, upon which to calculate the amount of rate alteration. It is absolutely necessary to estimate an animal's breathing rate immediately before each test, since the rapidity of normal respiration is liable to slight variations, not only from day to day, but from one part of an experiment to another. Some students of human respiration overlook the extreme significance of the normal rate in determining reactions, and compare directly the

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[1]Graber's negative results (*Grundlinien zur Erforschung des Helligkeits und Farbensinnes der Tiere, 102. Prag*, 1884) were probably due to the testing of many animals at once or to failure to change the glasses regularly.

[2]When shallowing accompanies quickening, the amount of respiratory activity may be no greater, or even less, than in the previous condition. But since there was generally no depth alteration after the first day, the quickening reported may be regarded as a fair measure of the influence of the stimulus.

TABLE II. RESPIRATORY REACTION TO COLORED LIGHT.

Animals		Average Rate per minute of each of 5 respiration before stimulus					Stimulus	Average Rate per minute of each of 10 respirations after stimulus									
		5	4	3	2	1		1	2	3	4	5	6	7	8	9	10
K	R	31.2	31.4	31.6	31.2	31.6	R	32.9	**33.7**	33.7	33.3	32.4	32.6	32.4	32.6	32.4	32.0
	Y	31.7	31.7	31.4	31.4	30.9	Y	**35.6**	35.5	33.5	32.9	32.9	32.2	32.0	32.8	31.4	31.7
	G	31.2	30.9	30.6	30.6	30.9	G	33.1	**33.5**	33.1	33.7	33.4	32.9	32.6	32.9	32.6	32.4
	B	31.7	32.0	31.6	31.2	31.2	B	33.1	**34.4**	34.3	33.8	33.8	33.1	32.8	32.4	31.9	32.0
L	R	34.4	34.0	34.0	33.3	33.8	R	38.2	38.4	**40.0**	39.7	39.2	38.4	37.5	36.8	37.0	36.4
	Y	33.5	33.3	34.3	33.8	33.4	Y	38.7	40.0	**41.3**	40.5	39.7	39.2	37.2	37.2	36.8	37.0
	G	33.3	33.1	32.8	32.6	32.9	G	37.5	38.8	**41.3**	40.8	38.4	37.7	37.2	37.0	37.2	37.0
	B	33.7	34.0	33.5	33.7	33.3	B	37.9	**39.4**	38.7	38.9	37.0	37.7	37.0	36.4	36.1	36.1
M	R	37.7	38.2	37.0	37.2	36.8	R	40.8	**44.4**	42.5	41.0	38.8	38.7	38.2	37.9	37.7	38.4
	Y	37.2	37.7	37.7	36.8	36.4	Y	41.0	**44.0**	43.4	40.2	40.0	39.7	38.8	38.8	39.4	39.7
	G	38.7	38.7	39.2	39.4	39.2	G	41.6	**44.0**	42.5	41.0	39.4	39.4	38.4	38.2	38.7	38.2
	B	38.2	38.2	37.0	37.2	37.5	B	41.3	**44.4**	43.8	42.5	41.3	39.4	39.2	38.7	38.2	38.2
N	R	31.2	30.7	30.7	29.9	30.6	R	33.5	**34.6**	34.4	33.8	32.8	31.9	31.6	30.9	31.2	31.0
	Y	31.9	31.2	31.4	31.6	31.6	Y	34.3	**37.9**	36.1	33.8	32.9	32.4	32.6	31.7	31.4	31.0
	G	30.6	31.2	30.6	30.3	30.0	G	34.8	**36.6**	34.0	32.9	32.4	31.7	31.9	31.7	31.2	31.9
	B	30.6	30.0	30.7	30.9	30.1	B	35.6	**37.7**	36.1	34.8	33.3	33.1	32.9	32.0	31.2	31.7
O	R	24.8	24.7	24.4	24.2	24.9	R	**27.0**	26.9	26.9	25.2	24.1	24.0	23.5	23.5	23.2	23.2
	Y	24.0	23.8	24.5	24.0	23.9	Y	25.4	25.4	**25.9**	25.5	25.5	25.1	24.5	24.5	23.5	23.9
	G	24.6	24.8	25.0	24.7	24.8	G	**28.3**	26.5	27.1	25.6	24.3	24.0	24.0	23.7	23.6	23.0
	B	25.4	25.4	25.5	24.4	23.8	B	**26.0**	26.0	25.8	24.8	25.0	24.6	24.7	24.0	23.7	23.8
P	R	23.5	23.7	23.6	23.1	23.0	R	25.5	**25.8**	24.8	24.4	23.3	23.1	23.3	22.7	22.8	22.1
	Y	23.6	23.6	23.6	22.8	23.5	Y	**26.9**	24.8	24.9	25.1	24.7	24.3	25.0	24.4	24.3	24.0
	G	24.5	24.1	24.5	23.3	23.6	G	**26.6**	25.3	24.6	25.0	24.2	24.2	23.7	23.3	23.8	23.4
	B	23.9	24.2	24.0	23.8	23.2	B	27.1	**27.5**	24.8	24.5	23.7	23.9	24.3	23.8	23.6	23.6

		first part					second part									
Q	R	25.6	24.9	24.9	25.0	24.4	25.8	25.5	25.0	25.2	24.4	24.2	23.6	24.2	24.0	23.7
	Y	25.9	25.3	25.3	25.0	25.0	26.8	25.5	25.6	25.6	25.0	24.4	24.6	24.2	24.4	24.0
	G	25.5	25.1	25.4	24.8	24.7	26.6	25.5	25.6	25.2	24.7	25.0	25.1	24.3	24.4	24.3
	B	26.1	26.0	25.6	25.0	24.8	26.3	25.8	25.6	25.0	24.5	24.2	24.3	23.9	23.8	23.4
R	R	26.3	26.8	26.3	26.6	26.3	27.9	27.4	27.4	26.4	26.2	25.8	26.2	26.0	26.1	26.2
	Y	26.8	27.1	27.1	27.0	27.0	27.5	27.5	27.4	26.8	26.6	26.9	26.4	26.4	26.5	26.0
	G	27.1	27.3	27.3	26.6	26.4	27.1	26.9	26.9	26.0	26.2	26.2	25.9	26.3	25.8	25.5
	B	27.4	27.1	27.0	27.0	27.0	28.1	27.4	27.0	26.8	26.4	26.4	26.3	26.3	26.2	26.2
S	R	30.3	30.4	29.7	29.4	29.9	31.4	30.9	30.3	30.0	29.4	29.0	29.6	29.6	29.4	29.0
	Y	30.3	30.3	30.1	29.6	29.7	31.4	30.7	30.3	30.0	29.9	28.8	29.1	29.0	29.0	28.4
	G	30.1	30.3	30.1	29.4	28.8	32.6	31.7	31.0	30.9	30.6	29.9	29.9	29.1	29.0	29.0
	B	30.6	29.6	31.2	29.7	29.0	32.8	32.4	31.4	30.0	29.1	29.1	29.0	29.6	28.5	28.5
T	R	30.1	30.0	29.6	30.1	29.9	32.4	**32.0**	31.2	30.9	30.6	29.9	29.6	29.3	29.1	29.4
	Y	30.9	30.3	30.3	30.4	30.3	33.3	**32.2**	30.1	30.4	30.1	30.1	30.1	29.9	29.1	29.4
	G	29.9	29.6	29.6	29.9	29.1	30.1	**32.1**	30.6	30.3	30.1	29.0	29.1	29.1	29.0	28.7
	B	29.7	29.6	29.4	29.1	29.4	31.4	**32.6**	30.3	30.0	30.0	29.4	29.4	29.1	29.3	28.7
Average		29.6[1]	29.5	29.5	29.2	29.1	31.7	**32.2**	31.8	31.1	30.4	30.1	29.9	29.7	29.5	29.3

[1]This line of average was obtained from the four lines directly above. The first part shown the gradually diminishing influence of sound and jar of kymograph; the second, the immediate reaction to light stimulus, and the recovery therefrom.

reaction part of one breathing curve with the reaction part of another, and thus reach utterly unjustifiable conclusions.[1] We may even question the accuracy of comparing reactions after they have been severally expressed as percentages of their respective rates immediately before stimulation, for this procedure assumes that a given percentage of rate variation has the same meaning regardless of considerable differences in normal rates.   Although the gain is the same, we cannot be sure that a rise in rate from 25 respirations per minute to 27.5 per minute, for example, has the same significance as an increase from 35 to 38.50. The possible error arising from this source in the present investigation is lessened by the fact that, in case of any one animal, the average normal rates did not differ greatly, as will be shown in the tables.

1.   Reactions to light of different quality.   Each of the ten animals used was stimulated once daily for 25 successive days with red, yellow, green and blue light.   To prevent the order of stimulation from influencing the reactions, this was changed each day.   The colors were given the first day in the succession red, yellow, green and blue ; the second, blue, green, yellow and red ; the third, yellow, red, blue and green ; the fourth, green, blue, red, yellow ; the fifth, the same as the first, and so on to the end of the series.   The tracings were measured directly to half mm., and the rates before and after stimulation were arranged under the four colors.

The general statement of results is made in Table II. The averages were computed from a total of 15,000 measurements. The line at the bottom of the table shows a constant decrease in the breathing rate before the stimulus (29.6, 29.5, 29.5, 29.2 and 29.1).   This condition was probably due to the gradually diminishing influence of the kymograph, whose start at the beginning of a record always produced a temporary disturbance. Each animal showed a quickening in rate after stimulation. The average maximum reaction was attained in the second respiration (32.2), though individual birds varied in this respect.

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[1]FÉRÉ, loc. cit.

TABLE III. Respiratory Reactions in Percentages.

Animal	Normal Rate	Stimulus	Rate of 3 respiration after stimulus			Actual Rise[1]	% of Rise
K	31.4	R	32.9	33.7	33.7	2.3	7.3
	31.2	Y	35.6	35.5	33.5	4.3	**13.8**
	30.8	G	33.1	33.5	33.1	2.7	8.8
	31.2	B	33.1	34.4	34.3	3.2	10.3
L	33.6	R	38.2	38.4	40.0	4.8	14.3
	33.1	Y	38.7	40.0	41.3	6.9	**20.8**
	32.8	G	37.5	38.4	41.3	5.6	17.1
	33.5	B	37.9	39.4	38.7	5.9	17.6
M	37.0	R	40.8	44.4	42.5	7.4	20.0
	36.6	Y	41.0	44.0	43.4	7.4	**20.2**
	39.3	G	41.6	44.0	42.5	4.7	12.0
	37.4	B	41.3	44.4	43.8	7.0	18.7
N	30.3	R	33.5	34.6	34.4	4.3	14.2
	31.6	Y	34.3	37.9	36.1	6.3	19.9
	30.2	G	34.8	36.6	34.0	6.4	21.2
	30.5	B	35.6	37.7	36.1	7.2	**23.6**
O	24.6	R	27.0	26.9	26.9	2.3	**9.3**
	24.0	Y	25.4	25.4	25.9	1.4	5 8
	24.8	G	28.3	26.5	27.1	1.7	6.9
	24.1	B	26.0	26.0	25.8	1.9	7.9
P	23.1	R	25.5	25.8	24.8	2.7	11.6
	23.2	Y	26.9	24.8	24.9	1.6	6.9
	23.5	G	26.6	25.3	24.6	1.8	7.7
	23.5	B	27.1	27.5	24.8	4 0	**17.0**
Q	24.7	R	25.8	25.5	25.0	.8	3.2
	25.0	Y	26.8	25.5	25.6	.5	2.0
	24.8	G	26.6	25.5	25.6	.7	2.8
	24.9	B	26.3	25.8	25.6	.9	**3.6**
R	26.5	R	27.9	27.4	27.4	.9	**3.4**
	27.0	Y	27.5	27.5	27.4	.5	1.9
	26 5	G	27.1	26.9	26.9	.4	1.5
	27.0	B	28.1	27.4	27.0	.4	1.5
S	29.7	R	31.4	30.9	30.3	1.2	4.0
	29.7	Y	31.4	30.7	30.3	1.0	3.4
	29.1	G	32.6	31.7	31.0	2.6	8.9
	29.4	B	32.8	32.4	31.4	3.0	**10.2**
T	30.0	R	32.4	31.9	31.2	1.9	6.3
	30.4	Y	33.3	30.6	30.1	.2	.7
	29.5	G	30.1	32.6	30.6	3.1	**10.5**
	29.3	B	31.4	30.9	30.3	1.6	5.5
Average	29.06	R	31.54	31.95	31.62	2.89	9.94
	29.16	Y	32.09	32.19	31.85	3.03	10.39
	29.11	G	31.83	32.14	31.67	3.03	10.41
	29.07	B	31.96	32.59	31.78	3.52	**12.11**

[1]Using second respiration, as explained above.

Later the rate constantly diminished again toward the normal, which was almost reached by the tenth respiration. Animals differed widely also in sensitiveness. Some, for example Q and R, gave very weak reactions, and their rate soon returned to the normal, or even went below it ; whereas others, for example M and N, gave vigorous responses and did not regain the normal rate by the tenth respiration.

Table III shows the percentages of reaction given by each bird. Although the respiratory rate before stimulation differed considerably from animal to animal, the four normal rates for each subject (before the four kinds of light stimulation) were usually in fairly close agreement. Thus the rates for S were 29.7, 29.7, 29.1 and 29.4 ; for P, 23.1, 23.2, 23.5, 23.5 ; for all, 29.06, 29.16, 29.11, 29.07.[1] This general harmony warrants the belief that we have a fairly reliable basis upon which to estimate the amount of reaction. Since the average maximum reactions all occurred in the second respiration, it seemed best to use this respiration throughout in estimating the reactions of individual birds. This reduced the amount of reaction in some cases, but it gave uniformity of treatment by placing each response at approximately the same distance from the beginning of the stimulation. The percentages thus obtained show that a considerable difference existed among the subjects, although there was clearly a greater sensitiveness to blue than to red. For, while four animals were most sensitive to blue and only one least sensitive to this color, only two animals were most sensitive to red, and three were least so. Yellow caused the highest reaction with three birds, but occasioned the lowest in case of five others. One bird gave its highest reaction to green ; another its lowest to this color. The relative stimulating power of the four kinds of light is brought out more clearly in the final averages, which indicate a gradually increasing color sensitiveness as we pass from the red end of the spectrum to the blue, though there is little difference in the stimulating power of yellow and green.

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[1] These general averages are carried out to the second decimal place ; this did not seem necessary in case of individual birds.

The figures in Table II indicate that the animals recovered more quickly from the effect of red light stimulation than from the effects of other kinds. The average rates for blue in the recovery are sometimes less than for yellow and green, but they are always greater than for red. Yellow retained its stimulating effect longest.

Putting together the average results of Tables I and III we have the following comparison :

	R	Y	G	B
Total Color Choices of five animals	72	129	167	172
Respiratory Quickening of ten animals	9.94%	10.39%	10.41%	12.11%

It will be seen that there is a direct correspondence between the two sets of results, although the proportions do not hold, since the figures representing the breathing reactions to red and to yellow, or to yellow and to green, lie much nearer together than do the corresponding color choices ; and since, also, those representing the choices of green and blue are much more nearly equal than the corresponding respiratory percentages. The five pigeons used in the experiment first reported were not employed in the second, but they were the same species and had been raised in the same cote and general surroundings. Hence, we should probably be justified in inferring, on the basis of two sets of data, that *increased respiratory activity is a sign of agreeable stimulation* in pigeons as in man,[1] and this especially if we recall that the amplitude of the animals' breathing curve, when varying at all, generally became shallower, and that frequently certain minute irregularities of contour were noticed, as often occurs in human respiration during stimulations of a pleasant character.

2. *Reactions to light of different intensity.* Only four animals were used in this part of the investigation. Each was

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[1]Zoneff and Meumann, op. cit.

Angell, J. R. and Thompson, H. B. Organic Processes and Consciousness. *Psychological Review,* **6,** 32-69, 1899.

Isenberg, D. und Vogt, O. Athmung, *Zeitschrift f. Hypnotismus,* **10,** 131-158, 1900.

given five stimulations daily with light of one color. The stimuli were given one minute apart. Three different intensities 1, 2 and 4, were used, one being employed each day. The different intensities were given in the following order : two, four, one, two, etc., and the trials were continued until records were secured of twenty five reactions to each of the three intensities. The results were then tabulated in two distinct groups. One shows the rise of breathing rate under the influence of each of the three intensities (Table IV), and the other indicates the effect of repetition of the same stimulus (Table V). In case of these tests the *first* respiration after the stimulus was used in calculating the reaction.

TABLE IV. RELATION OF INTENSITY TO REACTION.

Animals	Intensity	Normal Rate	Rate of 4 respirations after stimulus				Act'l Rise[1]	% of Rise
P	1	21.2	22.9	22.6	22.3	22.7	1.7	8.0
	2	20.6	21.7	21.9	21.7	20.9	1.1	5.3
	4	20.6	21.6	21.7	21.0	20.7	1.0	4.9
Q	1	21.9	22.7	22.1	22.3	22.3	.8	3.7
	2	22.8	23.3	22.8	23.1	22.0	.5	2.2
	4	21.5	22.3	22.5	22.5	21.7	.8	3.7
S	1	26.1	28.7	28.1	28.4	27.7	2.6	10.0
	2	30.5	32.7	32.3	31.6	30.1	2.2	7.2
	4	25.5	27.7	26.8	26.9	26.7	2.2	8.6
T	1	27.3	28.4	28.3	28.0	28.0	1.1	4.0
	2	28.1	28.8	28.5	28.5	28.5	.7	2.5
	4	26.4	28.4	28.5	27.6	27.4	2.0	7.6
Average	1	24.1	25.7	25.2	25.3	25.2	1.6	6.6
	2	25.5	26.6	26.4	26.2	25.4	1.1	4.3
	4	23.5	25.0	24.7	24.4	24.1	1.5	6.4

[1]Using first respiration, as explained.

The results expressed in Table IV are of a negative character (see last column). Whereas all four birds reacted more vigorously to intensity 1 than to intensity 2, three were more sensitive to intensity 4 than 2, and the final average showed the animals to be slightly more sensitive to the lowest intensity than to the highest. Results more satisfactory would probably have been secured from a larger

number of animals, or if the different intensities of the stimulus had been used on the same day. But the latter course would not have given opportunity for observing, at the same time, the influence of repetition.

It will be seen by Table V (last column) that there was a strong reaction to the first of the five stimulations, a less vigorous one to the second, and steadily increasing reponses thereafter (8.0, 3.7, 4.1, 5.7, 6.9). It is not surprising that the second

TABLE V. Effect of Repetition.

Animals	Number of Test	Normal Rate	Rate of four respirations after stimulus				Act'l Rise	% of Rise
P	1	21.3	22.8	22.3	23.6	22.2	1.5	7.0
	2	20.7	20.9	21.9	21.2	22.3	.2	1.0
	3	20.7	22.2	20.9	20.9	20.3	7.3	7.3
	4	20.7	22.4	21.9	21.7	20.8	8.2	8.2
	5	20.9	22.2	22.0	22.8	21.2	1.3	6.2
Q	1	22.3	23.0	22.7	22.3	22.0	.7	3.1
	2	21.6	21.9	21.8	21.9	21.5	.3	1.4
	3	22.1	22.1	22.2	21.7	21.3	.0	0.0
	4	22.5	23.4	22.5	22.6	22.6	.9	4.0
	5	21.9	23.5	23.1	22.9	23.0	1.6	7.3
S	1	28.3	30.4	30.2	28.6	27.5	2.1	7.4
	2	27.3	29.7	29.2	28.6	28.9	2.4	8.8
	3	27.3	28.8	28.1	28.7	27.4	1.5	5.5
	4	27.2	28.8	28.4	28.8	28.2	1.6	5.9
	5	27.7	30.6	29.5	29.9	28.9	2.9	10.5
T	1	27.3	29.0	29.5	27.6	29.9	1.7	6.2
	2	27.7	28.3	28.3	29.4	28 0	.6	2.2
	3	26.8	27.6	28.0	26.9	27.6	.8	3.0
	4	27.6	29.0	28.0	28.6	28.3	1.4	5.1
	5	27.6	28.5	28.1	27.9	27.3	.9	3.3
Average	1	24.4	26.3	26.2	25.5	22.5	1.9	8.0
	2	24.3	25.2	25.3	25.3	25.2	.9	3.7
	3	24.2	25.2	24.8	24.6	24.2	1.0	4.1
	4	24.5	25.9	25.2	25.4	25.0	1.4	5.7
	5	24.5	26.2	25.7	25.9	25.1	1.7	6.9

reaction was weaker than the first, since the animals were better prepared for the second stimulus. That there was an increased amount of reaction thereafter is probably to be accounted for, partially on the basis of summation of stimuli, and partially in view of the fact that the short illuminations may have

occasioned mental action, thus indirectly favoring quickened respiration. These stimuli are not comparable to the meaningless pistol shots before mentioned, to which as we saw, the breathing curve quickly became insensitive. They are rather to be classed, though not in themselves of a significant character, with the cage sounds (cooing flapping, etc.), which never lost their disturbing influence upon the respiration. For the short flashes of light probably gave the animal *glimpses* of its prison, *increased desire* to escape, etc., in a word, *meanings*, which involved heightened, rather than depressed, breathing activity, and worked directly against the dulling tendency of repetition.[1]

It is to be noticed that the normal breathing rates of the four animals used in this series of tests were considerably lower than those for the same birds in the preceeding series. P's average normal rate diminished from 23.3 to 20.9; Q's, from 24.9 to 23.1; S's, from 29.5 to 27.6; and T's, from 29.8 to 27.4. This decrease was probably due to the animals' getting more and more accustomed to the general conditions of the experiment, and thus giving a less quickened, or disturbed, rate when attached in the nest and before being stimulated.

VI. Summary.

1. The normal breathing curve in pigeons is very similar to that of the human subject, except that the rate is about twice as rapid. Respiration is sensitive to several kinds of stimulation, and shows various modifications, especially quickening, shallowing, deepening, pauses and irregularities of contour.

2. Mechanical jars, sounds, and, perhaps, odors, influence breathing profoundly, especially jars, often causing abrupt inhibitions and many irregularities.

3. Stimulation by light also disturbs the breathing, though

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[1] MacDougall, R. Physical Characteristic of Attention, *Psychological Review*, **3**, 159-180, 1896.

Binet et Courtier, Influence de la vie émotionnelle sur la coeur, la respiration, et la circulation capillaire, *L'Année psychologique*, 65-126, 1896.

much less than do mechanical stimuli. The reaction usually involves an immediate quickening of rate, varying with the color of the light, and occasionally diminutions of amplitude and minor irregularities of contour.

4. Since an agreement was found between the *color-preferences* and the increase in *breathing rate* caused by colored light, it would seem that *agreeable feelings are accompanied by respiratory quickening* (and perhaps by shallowing and irregularity).

5. Daily reactions of four birds to three intensities of light, one intensity per day, showed no direct relation between amount of stimulus and amount of reaction. The second daily reaction showed the influence of repetition, since considerably weaker than the first; but thereafter was seen a continuous increase in amount of response.

6. Meaningless stimuli, as pistol shots, quickly lose their disturbing influence upon respiration, although it remains sensitive to those of a significant character, such as noises made by other birds. A stimulus which no longer influences the breathing, will sometimes occasion disturbance if accompanied by a second stimulus, of another order, even though of weak intensity.

THE EFFECT OF THE BEARING OF YOUNG UPON THE BODY-WEIGHT AND THE WEIGHT OF THE CENTRAL NERVOUS SYSTEM OF THE FEMALE WHITE RAT.

By John B. Watson.

(*From the Neurological Laboratory of the University of Chicago.*)

With Plate VI.

By observations in this laboratory the results of which are as yet unpublished[1], the normal increase in the body weight of the female white rat, uninfluenced by the bearing of young, has been determined. In this connection, a question arose as to the effect on the body growth, if the females were allowed to breed normally. The present paper reports the results of an investigation carried out in answer to this question. In addition to the above, there arose the further question, as to the effect of the bearing of young upon the weight of the central nervous system, and on the percentage of water contained in it.

So far as the writer knows, only three men have published observations bearing directly upon the subject in hand ; viz., Edlefsen, Hensen and Minot.

Edlefsen recorded the changes in the weight of 7 female guinea pigs from birth to the end of their first pregnancy. Unfortunately he compared the weight of the females during pregnancy with the weight of the males of a corresponding age. He made two points clear: 1st, the actual growth of the female guinea pig is slower during the period of gestation than that of the males of the same age during the same time ; 2nd, that while the true body weight of the mother immediately after parturition is less than that of the male of corresponding age,

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[1]It is expected that the results of this investigation will be published at an early date.

still if we consider the weight of the mated females just at the end of the period of gestation (before partuition), or better if we add the weight of the young, immediately after birth to that of the mother, we shall find that the weight of the breeding female is in the ratio of 1.164:1 to that of the male. The relationship after parturition (not adding the weight of the young to that of the mother) is 0.848:1.

HENSEN in an *Anhang* to EDLEFSEN's work, made some observations upon a litter of 4 guinea pigs, 3 females and 1 male, in order to determine the relationships between the growth of unmated females and males and thus supplement the results of EDLEFSEN. To control his results he mated one of the females. The following table presents his conclusions:

	Mated female	Unmated female	Unmated female	Male	Ratio
1 day after birth	59 gr.	63 gr.	57 gr.	59 gr.	1:1.03:0.96:1
51 days after mating the one female	211 gr.	220 gr.	207 gr.	228 gr.	1:1.04:0.98:1.08
117 days (immediately after parturition)	435 gr.	468 gr.	407 gr.	582 gr.	1:1.08:0.94:1.34

The weight of the mother just before parturition was 612 grammes. In this table we find some slight ground for inferring that the males grow at least as rapidly as the unmated females. On the other hand, the figures point to the fact that breeding females, reckoning in the weight of their young, actually build up more bodily material, than either the unmated females or males during a corresponding period of growth.

HENSEN then tried to determine the total increase in weight of one mated female during the period of gestation, apart from the increase in weight of her young. He began his reckoning at the time pregnancy first became noticeable. This happened on the 28th day after conception. The female weighed 335 gr. at this age. In the remaining 39 days of pregnancy (28 + 39 days = period of gestation) she herself gained 100 gr. in weight and produced 146 gr. of bodily substances in young and adnexa, i.e. 1.46 times more than she herself gained.

MINOT tabulated the average changes in the weights of 66 female guinea pigs, from the beginning of the period of gesta-

tion to parturition, and then again for 35 days immediately after parturition. The usual length of the period of gestation is from 67 to 68 days.

The average weight of the 66 pregnant guinea pigs just before delivery was 830.2 gr. Their average weight 3 days after delivery was 588 gr. The average weight of unmated females at that age, he had previously determined from many observations to be 532.1 gr. Thus it appears that at the end of pregnancy, the breeding females were heavier than those not allowed to breed, by about 55.9 gr. MINOT's tables presenting the average alterations of weight of these 66 guinea pigs from the 35 days immediately after the delivery of their young, show that there is a very great loss of weight, especially marked during the earlier days of this period. Subsequently there is a slower loss in weight continuing for about three weeks, after which recovery begins.

Owing to the destruction of MINOT's pigs—the story of which has become classic in the annals of American research—further investigation of this subject was cut short.

If we compare the results of EDLEFSEN and HENSEN's observations on the growth of gestating guinea pigs during their first pregnancy, with those of MINOT, we find a contradiction. EDLEFSEN and HENSEN conclude that the growth of the gestating females, when considered apart from the young developing in them, is slower than that of either the unmated females or males. MINOT, on the contrary, concludes that the mated females immediately after partuition are heavier than the corresponding unmated females by 55.9 gr. On account of the large number of animals with which MINOT worked, his results are probably the more reliable.

Observations upon the Body-weight of the White Rat.

The writer's observations were begun upon a series of rats in the spring of 1903 and were continued for approximately one year. The females under observation were selected from five litters of rats born in April and May of that year. The

rats in these litters were of good stock, strong, healthy, and large for their age.

In the following description of results, these five groups are referred to under the letters A, B, C, D, and E. At the beginning of the experiments

Group	A	contained	5	female	rats
"	B	"	3	"	"
"	C	"	4	"	"
"	D	"	4	"	"
"	E	"	5	"	"
Total			21		

Each of the above-named groups, at 70 days of age (the age at which sexual maturity is reached), was divided into approximately equal sub-groups, one containing the rats which were to be mated, the other, those which were to remain unmated.

Since we desired to make the condition for growth as nearly ideal as possible, we fed the rats used in this experiment very carefully, giving them always a rich and varied diet. Baker's bread, softened with unskimmed milk, was the chief article of food. Since food of this character is likely to sour if left in the cages, only so much of it was given as could be consumed by the rats from one period of feeding to the next. Sunflower seed and cracked corn were always kept in the cages. Vegetables and meat were given once a week. Great care was taken to avoid surfeiting the rats. They were fed each morning between nine and ten o'clock.

The rats were weighed once a week, and weighing came always before feeding.

The experiment was conducted in a warm, sunny room, the temperature of which was kept constantly above 70° Fahrenheit.

At 70 days of age[1] the rats destined to bear young were

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[1] At this age the average weight of the unmated rats approximately equalled that of the mated. A slight difference, however, existed in favor of the mated rats (2 gr. heavier on the average).

mated with the largest males in the laboratory. (These males weighed about 400 grammes). The males were kept in the cages until the females showed signs of pregnancy, and were then removed. Twenty one days is the usual length of the period of gestation. In nearly every case large litters were born—in some cases the litters contained as many as 14 young. At the end of twenty days the young were removed from their mother. She was then allowed to recover completely. This took, usually, from 30 to 50 days. When recovery was complete, the males were again introduced, and the same routine followed, until each mated rat had born three litters. When recovery was complete from the birth of the third and final litter, the experiment, so far as the body-weight was concerned, was at an end.

The unmated rats, of course, kept to the even tenor of their way. The records previously referred to, show the normal rate of the body growth in the unmated females. In the present experiment we again recorded the weight of unmated females, in order to have a control series with which to compare the mated rats. By subjecting both the mated and the unmated rats to exactly the same conditions as regards food, temperature, etc., we hoped to be able to isolate the influence of breeding on the growth of the body, However, if one compares the growth-curve of the unmated rats in this paper with the records referred to above, it will be found that, notwithstanding the better quality of food used in the present case, no very great difference in the body growth in the two cases can be observed.

The following table presents for comparison the record of the weights, at the ages given, of the mated and unmated individuals of Group C. This table gives a good illustration of what occurred in the four other groups.

Plate VI shows separately in graphic form the changes in the body weight of each of the above mated and unmated rats of Group C.

A study of this table and plate shows the fluctuations in the body weight of the mated rats, due to pregnancy, suckling

of young, etc. The general features of the table are clear, but one point is worthy of note. Immediately after the birth of the young, the mated rats are much heavier than the unmated.[2] The mated animals, during pregnancy, seem to have the power of storing up in some way (fat?) the products obtained from

TABLE I.

Showing the average body weight, at the ages given, of the two mated and the two unmated rats of Group C.[1]

	Unmated	Mated	
At 70 days	116.1	120.9	Mated at this age.
81	129.4	129.1	Pregnant.
92	143.0	176.4	"
100	148.1	163.5	Young born 6 and 3 days before respectively.
107	150.9	170.6	
114	153.7	162.6	Young very large : removed.
121	160.1		⎫
128	162.5	174.6	⎬ Recovery.
135	162.8	170.7	
142	163.5	171.6	
149	163.1	169.0	⎭
156	168.1	176.5	Recovery complete.
163	168.5	184.0	Mated one day before.
170	169.3	204.2	Pregnant.
177	171.3	235.1	"
184	174.1		
191	177.4	218.8	Young born 12 and 5 days before, respectively.
198	177.6	227.6	
205	180.3	225.7	Young removed.
212	187.2	226.3	One rat ill.
219	190.1	226.0	" " "
233	190.8	222.5[1]	The sick rat had to be killed.
240	191.7	235.7	The average rose after killing the other rat.
247	193.3	220.2	Slightly ill.
254	194.0	226.0	Mated for third and last time.
261	198.6	235.8	Pregnant.
275	198.1		
282	192.4	239.0	A litter of 14 young was born 6 days before.
296	190.1		Exhausted : young removed.
317	185.1	217.0	Rapid recovery after removal of young.
345	197.1	219.4	Final average.

[1]The above average for the mated rats is based upon the record of two individuals until the 233rd day ; thereafter, upon one.

[2]MINOT : *op. cit.* There is one difference between the guinea pig and the rat as regards the loss of weight during lactation. The loss in the guinea pig is most rapid during the first three or four days after parturition. Just the

their food.[1] If one takes into account the great strain of suckling ten or twelve young for the period of twenty days, one can easily understand that some such provision as this is necessary. This surplus in weight is largely lost during the time the mother is suckling her young.

Observations upon the Nervous System of the White Rat.

As soon as the observations on the body growth were completed, the rats were killed, and the separate weights of the brain and spinal cord, together with the percentage of water in each of these parts were determined. The cord was severed from the encephalon at the tip of the *calamus scriptorius*. The spinal roots were cut as close to the cord as possible.

After the weight of the fresh brain and cord was found, the percentage of water present in each was determined. The fresh brains and cords were put in an oven and subjected for eight days to a constant temperature of 90° Fahrenheit. They were then taken from the oven and cooled for thirty minutes in a sulphuric acid drying-chamber. The weight of the dried brains and cords was found, and with this completion of the data, the percentage of the water present in each was determined.

Table II gives the final results for both the mated and the unmated series of rats, on the weight of the body, the weight of the encephalon and cord, and the percentage of water present in each.

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reverse is true in the case of the rat. The older the young of the rat up to 25-30 days, the greater the demand upon the mother's milk supply and the consequent increasing exhaustion of the mother. If the litter is large, the weight of the mother is sometimes reduced to a weight which is below that of the corresponding unmated rats. The explanation is, of course, that the young guinea pigs are relatively large when born and become independent of the mother much earlier than the young rats.

[1]MINOT. See reference above, p. 145.

TABLE II.

1. Final Body Weights.

	Mated: Average body weight.	Unmated: Average body weight.	Age when killed.
Group A[1]	(2 rats) 196.2 gr.	(2 rats) 206.9 gr.	380 days.
" B	(1 rat) 232.0 gr.	(2 rats) 197.0 gr.	361 days.
" C	(1 rat) 219.4 gr.	(2 rats) 197.1 gr.	345 days.
" D	(2 rats) 237.0 gr.	(1 rat) 203.0 g..	320 days.
" E	(2 rats) 246.0 gr.	(3 rats) 234.8 gr.	309 days.
Average	(8 rats) 226.2 gr.	(10 rats) 210.9 gr.	

2. Brain Weight.

	Mated: Average brain weight.	Unmated: Average brain weight.
Group A	(2 rats) 1.8152 gr.	(2 rats) 1.7461 gr.
" B	(1 rat) 1.7740 gr.	(2 rats) 1.7974 gr.
" C	(1 rat) 1.8108 gr.	(2 rats) 1.7972 gr.
" D	(2 rats) 1.8443 gr.	(1 rat) 1.8426 gr.
" E	(2 rats) 1.9820 gr.	(3 rats) 1.9576 gr.
Average	(8 rats) 1.8585 gr.	(10 rats) 1.8397 gr.

3. Spinal Cord Weight.

	Mated: Average cord weight,	Unmated: Average cord weight.
Group A	(2 rats) .6244 gr.	(2 rats) .5812 gr.
" B	(1 rat) .6047 gr.	(2 rats) .5983 gr.
" C	(1 rat) .5945 gr.	(2 rats) .5797 gr.
" D	(2 rats) .6400 gr.	(1 rat) .5989 gr.
" E	(2 rats) .6619 gr.	(3 rats) .6364 gr.
Average	(8 rats) .6317 gr.	(10 rats) .6025 gr.

4. Percentage of Water in Brain.

	Mated: Average percentage of Water.	Unmated: Average percentage of Water.
Group A	(2 rats) 77.24 gr.	(2 rats) 77.20 gr.
" B	(1 rat) 77.47 gr.	(2 rats) 77.28 gr.
" C	(1 rat) 77.72 gr.	(2 rats) 77.70 gr.
" D	(2 rats) 77.50 gr.	(1 rat) 77.40 gr.
" E	(2 rats) 77.56 gr.	(3 rats) 77.32 gr.
Average	(8 rats) 77.47 gr.	(10 rats) 77.37 gr.

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[1]The two mated females in Group A were not as healthy as the other rats used in this experiment. After giving birth to their young, sores nearly always appeared on their necks. These grew steadily worse until the young were removed. After removal of the young, the sores would heal over completely, only to reappear at the next period of lactation.

TABLE II—(Continued).

5.　Percentage of Water in Cord.

	Mated : *Average percentage of Water.*		Unmated : *Average percentage of Water.*
Group A (2 rats)	68.61 gr.	(2 rats)	68.44 gr.
" B (1 rat)	68.37 gr.	(2 rats)	68.06 gr.
" C (1 rat)	68.52 gr.	(2 rats)	68.69 gr.
" D (2 rats)	68.16 gr.	(1 rat)	67.88 gr.
" E (2 rats)	68.81 gr.	(3 rats)	68.23 gr.
Average (8 rats)	68.51 gr.	(10 rats)	68.29 gr.

Conclusions.

1.　The groups of mated rats grew to be somewhat heavier than the unmated groups.　This was found to be true in four out of the five groups, Group A being the exception (see note, p. 521).　The mated individuals were, on the average, 9 % heavier than the unmated.

2.　The mated rats had both absolutely and proportionately the heavier central nervous systems.

3.　The weight of the brain, in the mated rats, was however not so heavy as we should have expected from the body weight.　Assuming that the brain weight should increase among mature rats in proportion to the $\sqrt[4]{}$ of the body weight[1] and taking the unmated rats as the standard, we find that the brain weight observed in the mated rats would correspond to a body weight of 219.5 gr.　But the observed body weight is 226.2 gr.　We draw the conclusion that the mated animals were somewhat fatter than the unmated—a conclusion which harmonizes with the facts observed at autopsy.

4.　The spinal cord was disproportionately heavy in the mated groups.　From the laboratory records of *breeding females* of about the same weight, it appears that one gram of increase of body weight is accompanied by .0020 gr. of increase in the weight of the cord.　If we take the relation between the

[1]DuBois found that in man at maturity the brain weights were related as the $\sqrt[4]{}$ of the body weights.　Dhéré and Lapicque, have determined a like relation in dogs of different sizes.

increase in the body weight of Groups B and C as compared with D and E (A being omitted : see note p. 521) of both the mated and unmated series, we find that in this case the increase of one gram of body weight is accompanied in the mated series by .0032 gr. and in the unmated series by .0012 gr. increase in the weight of the cord or on the average by .0022—nearly the value found from the laboratory records. If, then, we consider that the removal of the excessive fat on the mated series would reduce its body weight to 219.5 gr. when the animals were in the same condition as the unmated series, then the difference in body weights between the two series amounts to 8.7 gr. which would call for .0191 gr. additional cord weight in the heavier animals. The observed difference in the two series is .6317—.6025 gr., or .0292 gr., which serves to show that the spinal cord of the mated rats is heavier than we should expect from their true body weight. Whether this excess has resulted from changes affecting the entire cord or only the lumbar regions, was not determined.

5. The brain and spinal cord of the mated individuals contained a slightly higher percentage of water. Only a single exception to this relation was found in the entire series of ten groups, namely in the case of the spinal cord in Group C.

6. In general the older groups had smaller brain weights than the younger. The diminution in brain weight according to age is nearly proportional in the mated and unmated groups. This change probably marks the beginning of senescence.

Résumé.

The effect of the bearing of young is to render the mated rats slightly heavier than the unmated—some of the excessive weight being due to the larger amount of fat present in the mated animals. The proportional brain weight is not appreciably affected, but the spinal cord is distinctly heavier in the mated series, thus making the central nervous system as a whole heavier. The percentage of water in both the brain and spinal cord is in nine cases out of ten greater in the mated groups. This is perhaps the most important difference estab-

lished by the foregoing investigation, but the interpretation must await a further study of the diminution of the percentage of water in the central nervous system with advancing age and the conditions which probably modify it. '

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PLATE VI.

Fig. I.

Mated and Unmated Female White Rats.
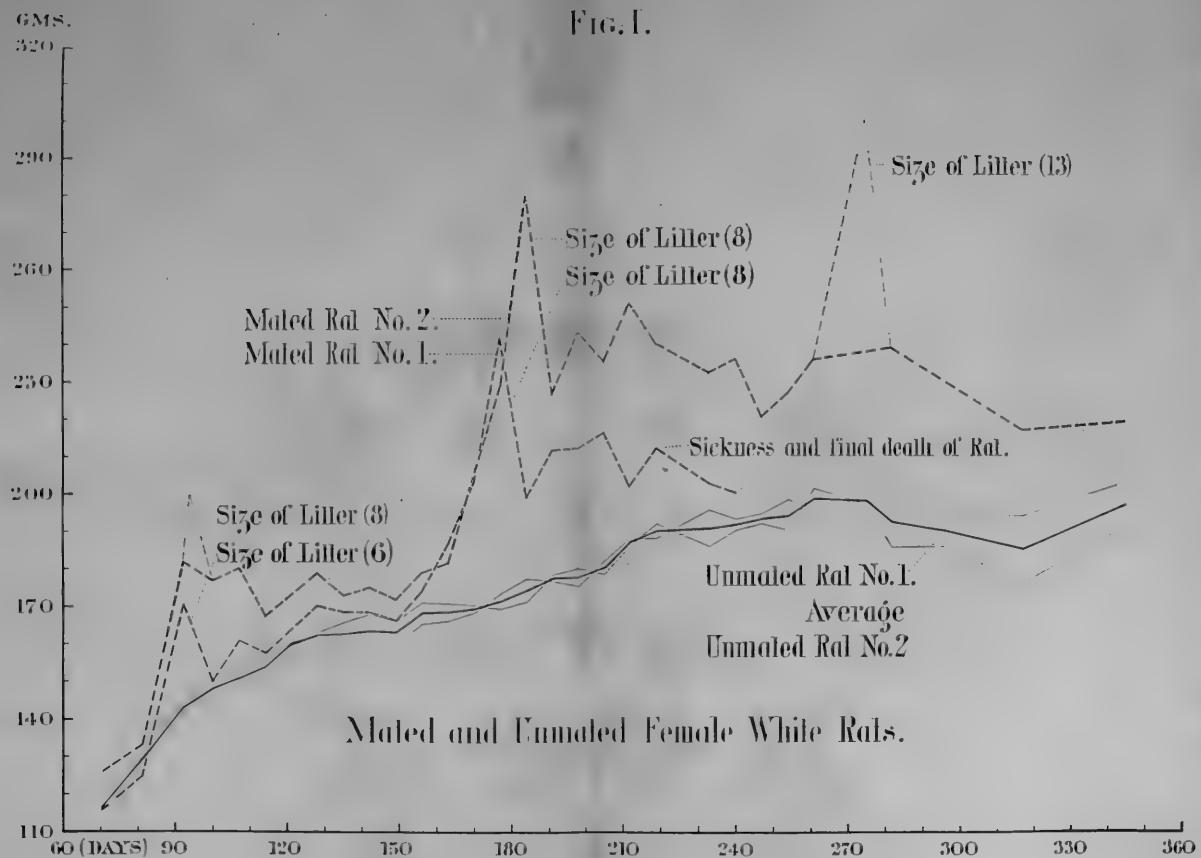
EDITORIAL.

THE WORK OF CARL WERNICKE.

In the death of CARL WERNICKE last spring the world lost one of its greatest students of the form and function of the human brain. Comparatively a young man, only fifty-seven, WERNICKE, as a result of an accident, met with while holidaying in the forest of Thüringen, was cut down at the height of his professional activity. The revision of his text-book on psychiatry, one of the most original and inspiring of modern works on the subject, occupied him just previous to his demise.

As a teacher, WERNICKE attracted many students to work under him personally ; he reached more through his published articles and books. As a personality, he possessed originality, independence and fearlessness, and accordingly came into conflict, sometimes bitter, with the opinions of other individuals of his time. As an investigator he leaves behind him a record of discoveries which will preserve his name permanently in the histories of brain-anatomy, brain-pathology, clinical neurology and psychiatry.

His life from his graduation on was devoted consistently to farthering progress in our knowledge of the brain. He began with brain-pathology, perfected himself in brain-anatomy, and did his best work in clinical observation.

Students of cerebral anatomy know WERNICKE especially through (1) his study of the gyri and sulci of the cortex cerebri, (2) his presentation of the microscopic features of the fibre-bundles of the brain as a whole, and (3) his atlas of brain-anatomy. He enriched our knowledge of cerebral topography by observing in the maze of sulcus variation the constants now designated as the sulcus occipitalis anterior, the sulcus occipita-

lis inferior and the sulcus fronto-marginalis. His contribution to the microscopic anatomy of the brain consists chiefly in his thorough presentation with valuation of the view points of embryology and phylogeny, of the totality of fiber-bundles, based upon the studies of MEYNERT, GUDDEN and FLECHSIG.

WERNICKE'S cerebral pathology was based upon anatomy and physiology. Indeed it is in the first volume of his "Diseases of the Brain" that his systematic description of microscopic anatomical structures is to be found ; this first volume is a collective review which may well serve as a foundation for all who desire to begin the serious study of the complexities of the cerebral conduction paths. His greatest single contribution to the pathological physiology and anatomy of the brain, was, undoubtedly, the discovery of the so-called "sensory aphasia" and the definite localization in the pallium of the area, diseases of which calls forth that now well-known and generally recognized syndrome. Studies in brain-histology proper seem to have interested WERNICKE much less than studies in gross and microscopic anatomy. Accordingly one finds but little mention of intraneuronal features in his writings. It was the grouping and chaining-together of neurones in greater complexes with formation of 'centres' and conduction-paths which appealed to him most, as was natural, perhaps, in a man so profoundly interested in cerebral localization and in the problems of aphasia and psychiatry as WERNICKE was.

The study of the aphasic symptom-complex which WERNICKE published in 1874 stands as an important pillar of support to modern clinical neurology. It was a research which ranks with the earlier studies of BROCA and SAX. It had not only a great neurological significance but exerted, through the analysis of the cortical processes which it embodied, an important influence upon the conceptions of physiological psychology. The demonstration of the continous process :—stimulus, sensation, memory-picture, association with other memory-pictures and motor projection, was first brought, as ZIEHEN points out, by WERNICKE, though the principles upon which it is based may be found in the investigations of others.

Hemiplegia, next to aphasia, is the subject in clinical neurology to which WERNICKE and his pupils have paid most attention with the interesting results known to all actively working neurologists. Following upon the researches of the CHARCOT school, WERNICKE's studies have gone far to extend our knowledge of the exact relations in that particular paralysis. Especially as concerns the residual paralysis during convalescence from hemiphlegia are the studies of WERNICKE and his pupil LUDWIG MANN of importance.

The latter part of WERNICKE's life was given over almost wholly to an attempt to found a scientific symptomatology of the psychoses, and it will generally be admitted, we think, that his greatest work is his 'Text-book of Psychiatry', which is wholly original, and widely divergent in the handling from that of any other psychiatrist, living or dead. WERNICKE in this treatise has made a book which will serve as a foundation for much of the psychiatric investigation of the future. Though written for students and physicians—the book bears the humble title of *'Grundriss'*—it makes profitable reading for even the most experienced alienist. Indeed, as SPENSER is sometimes called the poet's poet, it would not be surprising if WERNICKE came to be known as the psychiatrist's psychiatrist. He was an observer rather than an experimenter but those who knew him say that his talent for observation seemed at times to amount almost to divination.

Take him all in all, CARL WERNICKE was a man, whose like neurology and psychiatry will scarcely soon see again. He occupies a place among the few—with PINEL, with CHARCOT, with GRIESINGER and with MEYNERT.

LEWELLYS F. BARKER.

PAPERS ON REACTIONS TO ELECTRICITY IN UNICELLULAR ORGANISMS.[1]

No other field in the behavior of the lower organisms presents such puzzles as the reaction to the electric current. The continued activity in research and speculation along this line is therefore to be welcomed. Some of the papers recently published represent real advances in our knowledge; others do not.

Reactions to Induction Shocks. ROESLE (1) and STATKEWITSCH (2) find that the reaction of Paramecia and other infusoria to single induction shocks is essentially the same as the reaction to other usual stimuli. The animal swims backward, turns toward one side, then swims forward. Sometimes, according to ROESLE, the reaction is a simple forward movement, as is often the case with other weak stimuli. Both writers find the anterior end more sensitive than the rest of the body, save that ROESLE finds the region about the mouth still more sensitive; this is not confirmed by STATKEWITSCH. The reaction begins, according to STATKEWITSCH, with a reversal of the cilia at the anode; this spreads at once over the body, causing the start backward. With a stronger shock there is contraction and a discharge of tricho-

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[1] 1. ROESLE, E. Die Reaction einiger Infusorien auf einzelne Induktionsschläge. *Zeitschr. f. Allg. Physiol.*, Bd. 2, 1902, pp. 139-168.

2. STATKEWITSCH, P. Ueber die Wirkung der Induktionsschläge auf einige Ciliata. *Le Physiologiste Russe*, No. 41-45, 1903, pp. 1-55.

3. WALLENGREN, H. Zur Kenntnis der Galvanotaxis, I. Die anodische Galvanotaxis. *Zeitschr. f. Allg. Physiol.*, Bd. 2, 1902, pp. 341-384.

4. WALLENGREN, H. Zur Kenntnis der Galvanotaxis. II. Eine Analyse der Galvanotaxis bei Spirostomum. *Zeitschr. f. Allg. Physiol.*, Bd. 2, 1903, pp. 516-555.

5. STATKEWITSCH, P. Galvanotropism i Galvanotaxis Zhivotnyk. Chact pervaya. Galvanotropism i Galvanotaxis ryecnigatyx Infusorii. Dissertation. *Moscow*, 1903. 160 pp.

6. GREELEY, A. W. Experiments on the Physical Structure of the Protoplasm of Paramecium and its Relation to the Reactions of the Organism to Thermal, Chemical and Electrical Stimuli. *Biol. Bull.*, vol. 7, 1903, pp. 3-32.

7. BIRUKOFF, B. Zur Theorie der Galvanotaxis. *Archiv f. Anat. u. Physiol. physiol. Abth.*, Jhrg. 1904, pp. 271-296.

cysts at the anode. With a still stronger shock, trichocysts are discharged also at the cathode, and at a later stage, over the whole body.

Reaction to the Constant Current. WALLENGREN (3,4) studied the transverse electrotaxis of Spirostomum and the anodic taxis of Opalina. He finds that in both cases the current produces the same effect on the cilia as in the usual cathodic taxis. The cilia of the cathode region are reversed, striking forward, while those of the anode region strike backward. The taking of the transverse position (Spirostomum) and the movement to the anode (Opalina) are due to special peculiarities of the body structure and ciliary apparatus of the organisms. In a weak current Spirostomum, and in a stronger current Opalina, go to the cathode, like other Ciliata. It is evident from WALLENGREN's work that the fundamental phenomenon in electrotaxis is the action of the current on the cilia ; the direction of movement depends on more or less accidental conditions.

The work of STATKEWITSCH (5) is an extensive study of the reactions of many infusoria to the electric current, as part of a general examination of the reactions of animals to electricity. The work is careful and thorough ; the apparatus and methods are of the best ; all together it is exactly such a piece of work as was needed. It is to be hoped that the results may soon be published in a language that will make them more generally accessible.[1]

The work is filled with detailed observations of great interest ; we can mention however only a few of the general results. Twenty eight species of infusoria were studied, Paramecium serving as the main type in the detailed description. The current was found to have the same effect throughout. In the cathode region the cilia are reversed, while elsewhere they strike backward, as under normal conditions. With a weak current only a few cilia at the cathode tip are reversed ; as the current becomes stronger the reversal spreads toward the anode end. This account agrees throughout with the original one by LUDLOFF. Thus the cathodic reversal of the cilia is the one peculiar phenomenon in the reaction to the electric current. To it are due the characteristic features of the reaction, and it is this cathodic reversal that requires explanation. STATKEWITSCH made a thorough study of the internal chemical changes due to the current, by the use of ingested chemical indicators. It was found that the reaction of the endosarc becomes more alkaline under the action of the current, but this is not

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[1]Since this review was written a summary of parts of STATKEWITSCH's results have appeared in the *Zeitschrift f. Allg. Physiologie.*

limited to either end of the body. (The longitudinal rotation of the endosarc would prevent such limitation, even if the effect were primarily produced at one end.) STATKEWITSCH concludes that the reversal of the cathodic cilia is due to an interference with the metabolic processes, showing itself in this greater alkalinity.

Of observations on subordinate points, the following are interesting. If the current is frequently reversed, the organisms maintain a transverse position. A careful study of the contraction at the anode and swelling at the cathode led to the conclusion that these could not be accounted for by the direct cataphoric action, but depend on the vital contractility of the protoplasm. The electric reaction was shown to be independent of rheotropism. A particularly careful study was made of the reactions of infusoria in solutions of chemicals. The animals were gradually acclimatized to the solutions, and it was then found that the reaction to the electric current is the same as in ordinary water. It is only when the infusoria are first introduced, and are inclined to swim backward as a result of the chemical stimulation, that they swim in the current backward to the anode.

As a result of his work, STATKEWITSCH rightly insists that "the effect on the cilia is the first and fundamental phenomenon of galvanotropism." This is evident indeed from all thorough observations on the subject, from those of LUDLOFF through the work of PEARL, WALLENGREN and others, to this work of STATKEWITSCH.

GREELEY (6) attemps to bring the reaction of Paramecium to the electric current in some way in relation with the electric charge which he supposes the particles of protoplasm to carry. In Paramecia from normal alkaline or neutral cultures he holds that the protoplasm is a colloid whose particles carry a negative charge. Such a colloid is liquefied by anions and by the cathodic effect of the current (that is, the effect produced on the end next the cathode); coagulated by cations and the anodic effect of the current. In Amoeba this would result in a solidification and contraction of the anodic side, with a liquefaction, decrease of surface tension, and flowing out on the cathode side ; hence according to GREELEY, the movement of Amoeba to the cathode. How similar factors could bring about the observed movement of Paramecium to the cathode GREELEY makes no attempt to show, but he holds that in some way this does occur. "The ultimate determining factor of the response to the electric current must be the electrical condition of the protoplasm itself." The essential point in GREELEY's view is the following : "In every case the reaction of a Paramecium to an external stimulus leads it to remain under those conditions which

liquefy the protoplasm. Attraction is accompanied by liquefaction, repulsion by coagulation." This generalization GREELEY applies to all reactions, specifying particularly those to heat and cold and chemicals, as well as the reactions to electricity.

How far are the facts in agreement with this generalization? Is it true that the animals always move toward liquefying conditions, and away from those causing coagulation?

1. GREELEY says that in the reaction to the electric current "a dense gathering occurs about the negative electrode. In other words they collect at that point in the electrical field where the conditions are such as to induce a liquefaction of the protoplasm." Now it has long been known that this gathering about the cathode is a secondary and accidental result of the orientation produced by the current, and it does not occur if the cathode is so placed that the organisms can get past it. When this is possible, they swim behind it, into a region where there is no current. There is thus no tendency to collect where liquefaction is produced. All throrough work shows that the effects of the current on the cilia, resulting in orientation, are the fundamental features, and any gatherings produced in one place or another are a secondary result.

2. In a stronger current the organism becomes oriented, but does not move either to the region causing liquefaction, or to that causing coagulation. It remains in place, the cilia of the two halves of the body driving it with equal force in opposite directions.

3. With a still stronger current the animals swim backward to the anode, though liquefaction is still caused at the cathode and coagulation at the anode. This behavior squarely contradicts GREELEY's generalization.

4. GREELEY holds that the movement backward to the anode in acids and osmotic solutions is in agreement with his theory, holding that the electrical condition of the protoplasm has become reversed, so that now liquefaction and coagulation occur under opposite conditions. But GREELEY does not show that under these conditions coagulation occurs at the cathode, liquefaction at the anode, as his theory requires, and no one has ever reported anything of the sort. Further it is established that as soon as the organisms become acclimatized to the solutions, they go to the cathode, as usual. There is no explanation of this fact, on GREELEY's theory.

5. GREELEY seems not to recognize that some of the supposed facts on which he bases his generalization are contradicted by the results of previous investigators. He says that Paramecia from

normal alkaline cultures are positive to alkalies (which cause liquefaction), and negative to acids (which cause coagulation). The present reviewer emphasized in his first paper on the reactions of Paramecium (Journ. of Physiol., vol. 21, p. 268, p. 317) a result that is precisely the opposite of this. Paramecia from alkaline cultures were found to be negative to alkalies and positive to weak acids. From the results of literally thousands of experiments, many made since GREELEY'S work appeared, I am compelled to reaffirm this result. Paramecia then are positive to acids, which, as GREELEY finds, are coagulative in their effects.

6. Paramecia in acid cultures are, according to GREELEY himself, positive to acids. Yet acids cause coagulation under all circumstances, again according to GREELEY.

7. To strong alkalies Paramecia are under all circumstances negative. Yet strong alkalies cause liquefaction. This shows that liquefaction is not the ultimate determining feature in the positive reaction.

8. To all substances mentioned on page 11 of GREELEY'S paper as causing liquefaction, Paramecia are negative, while to a number of those listed as causing coagulation they are positive.

GREELEY'S generalization is therefore in direct conflict with many of the best known facts in the behavior of these organisms. It is no doubt true that as a rule Paramecia avoid strongly coagulating agents, for they avoid most injurious agents, and coagulation of the protoplasm is one of the commonest injuries produced by external agents. But they equally avoid agents that cause liquefaction beyond a certain stage, and they react in the same way to many conditions that are not known to cause either liquefaction or coagulation.

The only basis on which GREELEY'S theory might give a plausible generalization as applied to electrotaxis would be the following. It might be said that liquefaction, produced at the cathodic end of the organism, is connected in some way with the reversal of the cathodic cilia. But under other circumstances the cilia are reversed when there is no indication of liquefaction, as in swimming backward in a strong acid which causes coagulation.

The paper of BIRUKOFF (7) is a defence of the theory that the movement of infusoria to cathode or anode is due to a passive transportation by the cataphoric action of the current. Since Paramecia in ordinary water go to the cathode, while in salt solution they go (according to BIRUKOFF) to the anode, the amount of electromotive force developed on the bodies of the animals during the passage of the cur-

rent should be different in the two cases. The experimental portion
of the paper consists in a demonstration, by means of fitting apparatus
that this is actually the case.

This result shows only that there is nothing in the conditions to
make such movement as BIRUKOFF assumes *a priori* impossible. It
of course by no means shows that electrotaxis actually takes place in
the way BIRUKOFF supposes. BIRUKOFF's theory for these conditions
is really completely disproved by the fact, set forth by PÜTTER and
others, that after the Paramecia have been for a short time in the salt
water, so as to become accustomed to it, they no longer go to the
anode, but as usual to the cathode. BIRUKOFF of course recognizes
that this if true is fatal to his view. He attempts to meet it by as-
suming that PÜTTER's observations were due to preposterously crude
experimental errors, and that the facts are not really as PÜTTER states.
But the facts have been established beyond doubt, not only by the
observations of PÜTTER, but by the careful work of STATKEWITSCH
above set forth. The present writer can testify from his own observa-
tions to the accuracy of their accounts.

It seems incredible that anyone should yet, after all the thorough
work that has been done on the movements of the cilia, hold that the
movement to cathode or anode is a passive one, due to the cataphoric
action of the current. This possibility is of course the first one to
occur to the observer, and it is the first one to be dismissed after the
facts are carefully observed. Before the current is passed through
them, the infusoria are moving about in all directions. Now the cur-
rent is closed, and all continue to move at approximately the same
rate as before, but they all now swim towards the cathode. There is
then not the faintest shred of evidence that the movement is due to
cataphoresis. The movement existed before the cataphoresis came
into effect; the only essential difference between the later motion and
the first one (with one exception to be mentioned) is that the move-
ment is now directed toward the cathode. The observed movements
of the cilia, which are demonstrated by the currents produced to be
powerful, *must* cause the animals to move forward, just as when no
electric current was acting. There is no reason whatsoever for calling
in the cataphoric action to transport the animals; there is nothing for
it to do.

The one difference in the movement of the cilia is the fact that
some of the cathodic cilia show a reversed stroke. Neither BIRUKOFF
nor anyone else has attempted to show how this can be a direct effect
of cataphoric action. The observed movements of the cilia account

fully for the movements to cathode or anode. The turning into orientation is likewise fully accounted for by the opposed movements of cathodic and anodic cilia. BIRUKOFF seems inclined to doubt the observations of LUDLOFF on this point, but these observations have been confirmed by many investigators, and there is really not the slightest difficulty in repeating them and perceiving their accuracy. What is not accounted for is of course the observed effects on the cilia, particularly the cathodic reversal. It is here that further investigations should take hold.

Though BIRUKOFF starts with the thesis that the movement is due to cataphoric action, one finds that he admits in the course of his somewhat rambling paper various other factors. All difficulties with his theory are solved by bringing in the conveniently vague "general irritability" of the organism as an additional factor. He even admits, toward the end, after many pages of argument against it, that the "polar stimulation" of VERWORN may have something to do with the matter. One wonders finally whether BIRUKOFF himself really believes that the movement is due to cataphoric action.

It is of course possible that cataphoresis acts in some way as a stimulus to produce the observed movements of the cilia, just as it is possible that the neutralization of electric charges in the protoplasm may be in some way connected with the movements. But neither GREELEY nor BIRUKOFF have even so much as attempted to show how this occurs. Little real advance in our understanding of the reaction to electricity is to be expected from writers who ignore the fundamental phenomenon—the peculiar action of the current on the cilia.

H. S. JENNINGS.

LITERARY NOTICES.

Nägel, W. (Herausgeber). Handbuch der Physiologie des Menchen. Dritter Band (Physiologie der Sinne), Erste Hälfte, XII + 282, 1904. *Braunschweig, Vieweg und Sohn.*

This first installment of NAGEL's "Handbuch" forms a little more than a third of the volume devoted to sense-physiology, and, except for two short introductory articles on the doctrine of specific energies (NAGEL, Berlin, pp. 1-15), and the psychology of the senses (v. KRIES, Freiburg, pp. 16-29), it is confined to physiological optics. SCHENCK (Marburg) presents dioptrics and the accommodation of the eye (pp. 30-90); NAGEL, the effects of light on the retina (pp. 1-108); and v. KRIES, visual sensation (pp. 109-282). Visual perception, and the nutrition and the protective organs of the eye are left for the second half of the volume and will not, therefore, be considered in the present review.

Both introductory articles deal with certain concepts common to all the senses. To place JOHANNES MÜLLER's doctrine of specific energies beyond dispute, it would be necessary to show that different stimuli, acting on the same nerve, produce the same sensation. NAGEL mentions that the only really clear confirmation of this kind is the taste sensations that result when the *chorda* in the *cavum tympani* is mechanically, electrically or chemically stimulated He concludes that while the doctrine, with certain reservations in the case of the lower senses, is doubtless in general valid, the efforts, dating from HELMHOLTZ, to show the existence of separate nerves with correspondent specific energies *within* the individual sense-organs are not successful ; for the differences in sensation may just as well be due to the differences in the outward stimuli as to the specific energies of the nerve fibers themselves.

v. KRIES's introductory discussion of the psychology of the senses is important chiefly as a general estimate of the value of psychological analysis for sense-physiology, a question which receives repeatedly more specific attention in his longer article on visual sensation. Of special interest is his view of the theoretical possibility of measuring sensations (FECHNER's Psychophysic Law), and his treatment of the theory of specific comparisons, i.e. comparisons between sensations

that are not wholly alike, ''but between which, in addition to a definite difference, a certain similarity exists" (p. 22).

The first two articles on vision proper, dioptrics (SCHENCK), and the influence of light on the Retina (NAGEL), bring up to date what is known about these more objective phenomena of physiological optics. A colored plate, in the latter, shows well the movements of the cones and the pigment of the retina.

Nearly two thirds of the present half-volume are occupied by v. KRIES's suggestive and subtle contribution to visual sensation. The essay is subdivided as follows: laws of color-mixture, visual sensations and their psychological ordering, dichromatic color systems, adaptation of the visual organ, eccentric vision, after-images, local and color changes in the disposition (Umstimmung) of the visual organ, temporal relations of the effects of light, induced light and color sensations, limits of perception and discrimination, modifications in the color sense brought about experimentally or by disease, effects of inadequate stimuli, review of the facts and the results considered with reference to the theoretical conception of the visual organ.

It is possible to consider here only two points,—the author's general methodological views, and his estimate of present achievements in fact and theory.

As to the first point, it is evident that at almost every step the author feels the necessity of separating sharply the psychological method, ''for which the mutual relations of the sensations are of chief importance, their dependence on stimuli, however, of lesser significance" (p. 109), from the physiological method, for which the paramount problem is the relation of the reactions of the visual apparatus, as indicated by the sensations, to its adequate stimuli, and of the resulting facts to the objectively demonstrable properties of the visual organs. An instance of the latter method is, of course, the attempt to refer ''day-vision" to the cones, and ''twilight vision" to the rods. v. KRIES admits the possibility of a psychological analysis of the sensations, but, since he questions certain current psychological inferences drawn from such analysis, and condemns attempts to reach, through a psychological ordering of the sensations, conclusions concerning the physiological processes involved, he is skeptical as to the value of the analysis. It is possible, for instance, with AUBERT and HERING, to pick out red, yellow, green and blue as four colors having no mutual resemblances in quality, but ''an unbiassed person would hardly select blue in complying with a request to designate a sensation which is the contrary of yellow" (p. 135). It is doubtful, namely, whether the

often accepted oppositional relation between red-green and yellow-blue owes its existence to aught inherent in the psychological analysis itself. Similar doubt besets other such conclusions. Considering, then, the uncertain charater of even the psychological inferences drawn from an analysis of the sensations, it is far more precarious to draw conclusions as to the physiological processes involved. The author's general attitude towards the whole question, aside from the specific case just referred to, is given in his introductory paper, already briefly mentioned, in connection with his discussion of the theory of specific comparisons. The point discussed is the validity of assuming, from the possibility of making comparisons of similarity between sensations unlike in quality (e.g. similarity in brightness of two different colors) the existence of identical psychological or *physiological* elements which determine such similarity. ''If a physiological or a pyschological theory leads us to assume in all [light] sensations a definite element, which determines our impressions of brightness, then we may, on the basis of the theory, correctly refer to the equality or inequality of that element; but we may not, conversely, deduce from the possibility of a brightness-comparison the *existence* of such an element'' (p. 28). The insistence is, it is clear, so far as physiological inference is concerned, on the use of only those physiological concepts in explanation which result logically from a physiological theory based on recognized physiological procedure (e.g. the response of a sense organ to its adequate stimuli), and not on detached psychological analysis.

The second point that I wished to bring forward,—v. KRIES's estimate of the achievements of research in visual sensation, may be best stated in his own language : ''If, in closing, we summarize how far theoretical concepts make it possible for us to elucidate and interpret the facts, and indicate, in general, the state of our problem, we may perhaps say, as of chief importance, that the view which we have characterized as 'Duplizitätstheorie' explains in a wholly satisfactory way a large number of functionally related phenomena   This theory regards the rods, containing visual purple, as the organs of 'twilight vision,' and the cones as mediating a relatively different mode of vision, which we have called 'day vision.'   One may further consider, in the light of a zone theory [Zonentheorie], the elements that mediate day vision as composed in their peripheral segments of red, green and violet components, on the relative degrees of activity of which the character of the sensations in part depends ; in part, however, on other [more central] factors, which lead us to assume special conditions of color vision [Farbigkeit], to distinguish, namely, on one hand a red-green

and on the other a yellow-blue sense. With these assumptions one may take account not, to be sure, of all, but nevertheless of a very great number of the known facts. We may, indeed, represent the protanopic [red-blind] and the deuteranopic [green-blind] visual organs as originating in a lack of the red and green components respectively, the 'rotanomale' and the 'grünanomale' in a variation in the nature of the red or the green component, and the color blindness of the eccentric regions of the retina, as well as acquired color blindness, in a lack of the more centrally conditioned red-green and yellow-blue senses; we are then in a position to represent simply the large number of facts that are found in the vision of these various individuals, or of the various parts of the visual organ, and to account for them, with simple presuppositions, in a way throughout and exactly (so far as we can say) in accord with experience."

To exhaust the significance of this passage would require a synopsis of the whole article. The essence of the "Duplizitätstheorie" (for which it is hard to find a good translation) is, however, that the retina is a twofold visual apparatus, the rods, capable of "dark-adaptation," mediating colorless light in the presence of weak stimuli (twilight vision), and the cones, scarcely influenced by such adaptation, mediating our ordinary color (day) vision. This is perhaps the most widely accepted assumption in visual sensation, and to v. KRIES is due the chief credit of its experimental development. The zone theory assumes the validity of the triple-component theory (YOUNG-HELMHOLTZ) for peripherally situated visual elements, the possibility, however, in order to explain certain facts referred to in the quoted passage, of a fourfold division of elements, which form the basis of AUBERT's and HERING's thought, for the central [brain] portions of the visual apparatus.

Since the article is in no sense a defence or a criticism of any exclusive theory, but rather a calm attempt to do justice, in both fact and theory, to the various and perplexing results of accomplished research, it would be inept, in this short review, to attempt to epitomize the arguments for or against the various theories. One feels, however, that the effect of v. KRIES's present contribution will be to win still more serious consideration for HELMHOLTZ's general point of view, and to raise further questionings as to whether HERING's theory can so legitimately account for the manifold facts as is often assumed. One awaits therefore, with considerable interest, the appearance of HERINGS' pronounced volume for "GRAEFE-SAEMISCH's Handbuch."

It is a pleasure to read v. KRIES; for, while the style is often involved (at least for a foreigner) and occasionally abstract, the exposition

is so objective, the discussion so subtle and free from polemic, the whole spirit so just, that one may well devote time and effort to master this latest and fullest review of visual sensation.

<div align="right">R. P. ANGIER</div>

Meehan, Joseph. The Berlin "Thinking" Horse. *Nature.* 1904, **70**, 602, 603.

Cole, R. Langton. Thinking Cats. *Nature*, 1904 **71**, 31.

Both of these articles were called forth by notes which had appeared in previous numbers of *Nature*. The first is in response to a note in Vol. 70, p. 510 (Sept. 22, 1904), stating that a committee which had examined the performances of a horse at Berlin, known as "Clever Hans," had decided that several remarkable things he was capable of doing were not "tricks," but "due to the mental powers of the animal." Mr. MEEHAN takes exception to this view on the ground that fully as wonderful performances of a horse named "Mahomet" he knows to have been *tricks* pure and simple, the horse being entirely dependent upon the prompting of his trainer. He cites also a similar case of a collie dog which could spell out words by selecting the proper letters of the alphabet, play a game of cards, etc., and explains that the trick was accomplished by slight and almost unnoticeable signals given by its trainer. Mr. MEEHAN mentions a cat which climbs a doorpost and opens the latch with her paw, and this he thinks "for a cat is more wonderful than are all the performances of the Berlin 'thinking horse' for a steed." It is apparently this observation which called out a note by "Y. N." in *Nature* Vol. 71, p. 9 (Nov. 3, 1904) and that referred to by the second title given above, both of which relate anecdotes which are supposed to bear on the "thinking" powers of cats.

<div align="right">LEON J. COLE</div>

van Rynberk, G. Tentativi di localizzazioni funzionali nel cervelletto. Archivio di Fisiologia, Vol. I, pp. 569-574, 1904.

The investigator follows the anatomical scheme of BOLK (Grundlinien der vergleichenden Anatomie der Säugetiere, Monatschrift für Psychiatrie und Neurologie, Bd. XII, S. 432, 1902) and finds that a partial lesion of the *lobulus simplex* of the cerebellum in the dog causes unstable oscillations of the head. From this he concludes that the *lobulus simplex* is the control center for the muscles of the neck.

<div align="right">J. C. B.</div>

Baglioni, Silvestro. Contributo alla fisiologia sperimentale dei movimenti riflessi ; specificità qualitativa degli stimoli e specificità qualitativa dei riflessi. Archivio di Fisiologia, Vol. I, pp. 575-585, 1904.

An interesting study of certain respiratory and other reflexes in

the frog, in which it is shown that the reflex follows only from a specific quality of stimulation, and that this arrangement is biologically useful to the animal. J. C. B.

Scaffidi, Vittorio. Sulla presenza di fibre efferenti nelle radici posteriorie e sulla origine delle fibre vasomotorie che si trovano in esse. Archivio di Fisiologia, Vol. I, pp. 586-603, 1904.

A good review of the literature on the posterior roots and an account of seven experiments on dogs, from which it appears that no true Wallerian degeneration follows an incision, that the degeneration observed is traumatic, and that therefore we are not justified in assuming the presence of efferent fibers. Further researches are necessary to settle the question of the origin of the vasomotor fibers found there.

J. C. B.

Parker, G. H. The Reversal of Ciliary Movement in Metazoans. *Amer. Jour. Physiol.* **13**, 1-16, 1905.

The author has demonstrated that reversal of ciliary movement, few instances of which are known among the metazoa, occurs in the labial cilia of *Metridium marginatum* under certain conditions. Experiments indicate that reversal is due to the action of potassium ions, in case of the substances tested, and not to osmotic action or mechanical stimulation. Reversal occurs only where the stimulus is applied, and there is no evidence of a nervous reflex. R. M. Y.

Pick. Des zones de Head et leur importance en psychiatrie. *Journ. de psychol. norm. et pathol.*, **I**, 113-117, 1904.

An account of a case of interest particularly to psychologists in showing that abnormal sensations may give arise to the most diverse and peculiar interpretations.

Some years ago HEAD pointed out that certain modifications of skin sensibility accompany derangements of internal organs (so called "zones of Head"). The case cited by PICK is that of a woman with hyperaesthesia in the region of the left breast, and with ideas of persecution, which, it was afterwards discovered, were due to the deranged sensations. The region of hyperaesthesia corresponded to that for the stomach, and further examination disclosed a dilatation of that organ. Under treatment, in a few days there was an amelioration of the stomach's condition and a disappearance of the delusions and sensory disturbances. S. I. F.

Wollenberg, R. Die Hypochondrie. Nothnagel's Specielle Pathologie und Therapie. Bd. **12**, Theil I, Abth. 3, pp. 66. *Wien, Hölder* 1904.

The author has given a satisfactory treatment of a very unsatisfactory subject. There is a great difficulty, sometimes impossibility, of

distinguishing between hypochondria and neurasthenia, and, in fact, hypochondria is not a disease entity, but only a psychopathic state, a morbid mental disposition of some kind. There are many varieties and fantastic aspects of the condition, but, in general, it may be said that the patient is usually depressed, and his attention directed chiefly to the condition of his body. WOLLENBERG rightly remarks that the cure comes 'not by means of physic, but by means of the physician.

<div align="right">S. I. F.</div>

Hellpach, Willy. Grundlinien einer Psychologie der Hysterie. *Leipzig, Englemann*, 1904, viii. + 502. Price M.9.

This is an exhaustively complete historical and analytical study of hysteria. Of its three chief parts the first deals with the problems of hysteria, the second, with the physiological and psychological phenomena included under this form of abnormal state or closely associated with it, the third, with the genesis of hysteria.

As space does not permit of an attempt to indicate the views set forth in the book, a list of the titles of chapters will serve to suggest the general plan of treatment. 1. The development of the problems of hysteria. This is chiefly an historical sketch. 2. The concept of disease. A thoughtful discussion of the concept of reactive and productive abnormality, and of the conditions which determine their use. 3. The logic of psychopathology. In this interesting epistemological study of the subject, of chief value to the pathologist, is a discussion of disease as a developmental concept. 4. Suggestion and psychic causality. An introduction to the author's analysis of hysteria. 5. The hysterical disturbances of movement. 6. The hysterical disturbances of perception. 7. The hysterical intellect. 8. The psychophysical obstacle before the psychology of hysteria. 9. The sources of hysteria. This chapter contains an account of the relations of the child mind to hysteria, and also of the bearing of " docility " upon this form of psychic abnormality. 10. The path to hysteria. 11. The development of the hysterical condition. 12. The social-pathological problem of hysteria.

The work gives an excellent history of the special problems under consideration, and a convenient bibliography of important literature. It is of equal interest to the psychiatrist, the psychologist and the epistemologist ; and one may venture the judgment that for all there is something of real value in the work.

<div align="right">R. M. Y.</div>

Bressler, Joh. Wie beginnen Geisteskrankheiten? *Marhold, Halle.* pp. 56. 1905.

Citing freely from such psychiatrists as KRAEPELIN, VON KRAFFT-

Ebing, Müller, Schüle, and others, the author enumerates with considerable detail the early symptoms of such typical nervous and mental diseases as dementia praecox, progressive paralysis, melancholia, mania, paranoia, neurasthenia, etc. From this array of evidence he concludes, 1st., That every mental disease begins with physical, especially nervous symptoms; 2nd., That no mental disease begins with a pathologically cheerful mood, except mania; 3rd., That in spite of the great differences observable in the fully developed forms of mental disease the early symptoms are to a large degree common and uniform. The author pleads for a larger number of public hospitals for the treatment of nervous affections which, if neglected, may readily develop into insanity.   J. C. BELL.

Sterzi, G. Intorno alla Struttura dell 'Ipofisi nei Vertebrati. *Atti Accad. Sci. Veneto-Trent.-Ist. Cl. Sci. Nat., I. Padua,* 1904. 9 text-figures.

This paper has a very wide range and includes the whole of the vertebrates from cyclostomes to mammals. A general scheme is given illustrating the rise of the hypophysis, from which it would appear that the organ is invariably formed of an epithelial and a nervous portion, the former of which being divided by its micro-chemical reactions into a chromophilous and a chromophobic section, of which the former increases and the latter decreases as we rise in the series. The paper is useful contribution to the comparative anatomy of the hypophysis.   F. J. C.

Sterzi, G. Morfologia e Sviluppo della Regione Infundibolare e dell' Ipofisi nei Petromizonti. *Arch. Anat. Embriol.,* **3,** 212. 6 plates and 3 text-figures. *Florence,* 1904.

In the first part of the paper after a short historical section the author describes the post-optic recess, saccus vasculosus, cavum corporis mammillaris (of Johnston's terminology) and hypophysis of *Petromyzon marinus,* subsequently comparing the latter with *P. fluviatilis* and *P. planeri.* He concludes that the hypophysis is a glandular organ, the secretion of which by its action on the blood capillaries has an effect upon the blood pressure. Part II contains a description of the development of the infundibular region in Ammocoetes of from 17 to 157 mm. The plates illustrate both parts of the paper.

    F. J. C.

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